

# The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

Arthur L. Schipper, *Editor*

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# The American Midland Naturalist

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## A Study of the Breeding Biology of the European Starling (*Sturnus vulgaris* L.) in North America<sup>1</sup>

Brina Kessel

University of Alaska, College

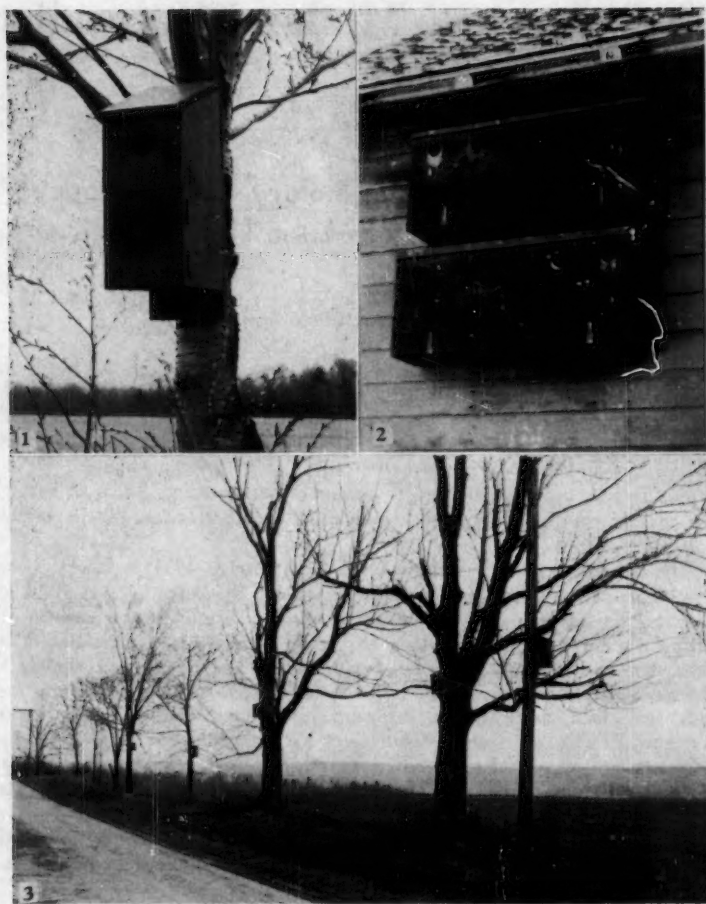
The European starling (*Sturnus vulgaris* L.) was first established in North America through introductions made in New York City in 1890 and 1891. Since its establishment much has been written concerning its migration and westward expansion of range, its nuisance habits of gregarious roosting and feeding, but almost nothing has been learned of its breeding biology. It is, indeed, paradoxical that so little is known of the breeding habits of a bird that has become so common and widespread and so economically important in North America.

The following study was made from 1945 through 1951 at Ithaca, New York, the more intensive work being done during the latter five years. The major portion of the study was carried out on a Study Area made up of starling nesting boxes placed along the roads bounding the periphery of a rectangular area, 1.4 miles long by .8 mile wide. The area was situated in a primarily agricultural district; there were some residences and farms along the roads, some fields under general cultivation, and some woodlots. Most of the area, however, was in scrubby pasture and hayfields, which were bordered by hedgerows and supported scattered trees, and, therefore, provided an excellent habitat for nesting starlings. The number of nesting boxes placed on the Study Area varied from seventeen in 1945 to a maximum of one hundred in 1947, when the boxes averaged about 230 feet apart; the number dwindled to sixty-nine by 1951. The manner of placement of the nesting boxes is illustrated in figures 1 and 3.

In the ensuing discussions on the breeding biology of the starling, summer observations include both resident and migratory populations, while the winter observations are limited to the resident portions of the population. During the breeding season the migratory and resident populations are indistinguishable; during the rest of the year the migratory birds lead a flock existence, and only the resident birds continue to exhibit breeding behavior about the nesting boxes.

*Acknowledgments.*—The major portion of this study on the European starling was made at the Laboratory of Ornithology, Cornell University, Ithaca, New York. It was initiated under the direction of Dr. Arthur A. Allen, to whom I would like to express sincere appreciation for guidance, assistance, and inspiration. I am indebted to Dr. P.

<sup>1</sup> Contribution from The Laboratory of Ornithology, Cornell University, Ithaca, N. Y.



Figs. 1-3.—1. Nest box used during studies on the breeding biology of the starling at Ithaca, New York, 1945-1951. Inside dimensions of the box were  $6\frac{1}{4}$  inches wide,  $6\frac{3}{4}$  inches deep, and  $15\frac{1}{4}$  inches high to the midpoint of the sloping roof; the hole was  $1\frac{3}{4}$  inches in diameter. 2. The colony nest box was used by only one pair of starlings at a time. 3. Placement of the nesting boxes on the Study Area at Ithaca, New York.

Paul Kellogg for the many ways in which he facilitated the study, and to Robert W. Dickerman for the many hours he contributed to gathering field data. I extend thanks to the many persons who assisted so freely in the various aspects of the field work, particularly to Dr. I. Pauline James, Dr. Elizabeth M. Boyd, Dr. Kenneth C. Parkes, Patricia Nutt Adams, Dr. Frances L. Burnett, and Dr. John F. Wanamaker who were especially generous with their time. I am further indebted to Dr. John L. Buckley and Dr. Richard H. Byrns for critically reading the entire manuscript, and to Dr. Joseph J. Hickey for reviewing the section on *Survival and Mortality*.

## BEHAVIOR DURING WINTER

After the period of minimal gonad activity in August, visits by the starling to the nesting sites become evident. Groups of males may sing in the tops of trees near the nesting sites, or individuals may sing and display in the immediate vicinity of the boxes; females are also evident about the boxes. The renewal of activities about the nesting sites during the fall and early winter is particularly evident during the morning hours at Ithaca, more especially between 7 and 11 A.M. Visits also occur during the day and in the late afternoon and evening, but with somewhat less regularity. The birds may spend long periods just outside the holes, frequently passing in and out. Old nesting material is often removed, and occasionally some new material is brought into the box. Some pairing seems to take place, and actual copulation has been noted during this period in Europe by Freitag (1939), Schüz (1942), Sopp (1932) and others. More often, however, the behavior indicates the main interest to be in the nest site rather than in a mate. Often only one bird will be seen at the nest site at a time, and males have been observed to chase the female away, and vice versa. Occasionally a female, singing and otherwise exhibiting male behavior, will establish and defend a nesting territory (Freitag, 1937, 1939).

Interest in the nesting sites is continued through the winter months, though considerably decreased during inclement weather. As the season advances, more and more time is spent about the nesting sites, and activities are intensified. The nest sites, however, still continue to be the point of attraction for the individual birds visiting them, even when both a male and a female visit the same box. In this latter case, the two birds are usually compatible, but independent. During the daytime, while away from the boxes, it is unlikely that the individuals of the "pairs" are associated. During mid-day visits, usually only one member of the pair is present at the box at a time; and the male and female usually arrive independently at the nest site in the evening, the male usually first. They also fly to the roost in the evening and return in the morning independently of each other.

In December some of the resident birds begin roosting in the boxes at night, instead of returning to communal roosts. By the middle of December small numbers of birds, consisting of both males and females, can be found thus occupying the boxes. On the evening of December 16, 1948, for instance, sixty-four boxes were examined for night-roosting birds. Six of these boxes had birds in them: two had a male and a female together in them; the others had singles, three of which were males and one a female.

Once the birds began roosting in the boxes in 1948-49, their numbers remained relatively constant on the Study Area until the middle of February. During the second half of February the number of roosting birds increased, reaching a peak in mid-March. The reason for this increase is not definitely known; it may have been due merely to the advancing season, or it may have been due to the spring migration of starlings from the south, though this increase in 1949 was somewhat early to have been caused by migration which was not obvious until about March 10. Late in March the number of roosting birds usually decreases, and between the time serious nest-building begins and the time of egg-laying few birds roost in the boxes at night (table 1).

A decrease in box roosting prior to egg-laying has been noted also by Schüz (1943).

During the months the starlings are roosting in the boxes, almost any pattern as to the sex or combination of sexes using a given box can be found. Females as well as males may roost alone in a box (another indication, incidentally, of the attachment of the birds to the box rather than to a sexual partner), or they may roost in pairs. In fifty pairs handled during 1948-1950 at Ithaca, forty-nine were composed of a male and a female, and one consisted of two males (table 1). Schüz (1942) never found two males roosting together, but he found two pairs consisting of females. During the present study, two birds was the largest number found roosting together in a box, but Schüz (1942) found three birds together in a box three different times. Unfortunately, each time, one of the birds escaped before examination. Of the remaining two birds, Schüz twice found two males, and once a male and a female. Schüz also cites Freitag as having once found four starlings roosting together in a hole.

In 1950 almost all the birds roosting in the boxes early in the season were "old timers" to the area. The banding of adult starlings at the nesting sites was begun during the spring of 1948, and was carried on intensively in 1949. It is safe to assume that by the end of the 1949 breeding season there were few breeding birds on the area that had not been banded. It is thus significant that on March 20, 1950, the first night check of the 1950 season, twenty-four birds were found roosting in about sixty-five boxes examined, only four of

TABLE 1.—Distribution of single and paired birds using the nesting boxes for roosting

Date	No. boxes examined	No. boxes in use	Single males	Single females	Pair	Total number roosting birds	Per cent boxes occupied
Feb. 2-4, 1948	57	12	1	4	5	12*	21.1
Mar. 6, 1948	35	13	3	1	8	21†	37.1
Apr. 8-15, 1948	60	7	1	2	4	11	11.7
Sep. 23, 1948	19	0	0	0	0	0	0
Oct. 29, 1948	21	0	0	0	0	0	0
Nov. 19, 1948	18	0	0	0	0	0	0
Dec. 16, 1948	64	6	3	1	2	8	9.4
Jan. 8, 1949	68	9	4	2	3‡	12	13.2
Jan. 29, 1949	60	7	3	0	4	11	11.7
Feb. 12, 1949	60	9	4	1	3	11	15.0
Feb. 26, 1949	55	15	2	8	4	18	27.3
Mar. 12, 1949	56	17	6	9	3	21	30.4
Mar. 24, 1949	55	9	3	2	4	13	16.4
Apr. 9, 1949	55	3	1	2	0	3	5.5

\* Includes two unsexed, single-roosting birds.

† Includes one unsexed, single-roosting bird.

‡ One pair consisted of two males.



which had not been banded in previous seasons. Of the four unbanded birds, one male and two females were judged to be yearling birds on the basis of their hackle feathers (see Kessel, 1951a). Later in the season the picture changed and many unbanded birds were found roosting in the boxes. On April 5, 1950, for instance, twelve birds were found roosting in the thirty boxes examined. Of these, only three were banded; and, of the nine unbanded birds, only one was a yearling. Evidently, with the progressing season and with migration (March 23, 1950) new birds, probably second-year birds that have not bred previously, move into the area, taking boxes that are not already occupied by the "old timers" that have been roosting in the boxes since early winter.

During the three months or more that the starlings are roosting in the boxes at night, a given bird may change its roosting site and shift its partner several times. The pattern of winter roosting, when viewed from the standpoint of a single box, vividly illustrates the amount of shifting that may be found. A single male, for instance, was found roosting in one box on December 16, 1948; but on January 8 this male had left, and another male with a female was roosting in the box. On February 26 a different female was roosting alone in the box, and on March 12 still another single female occupied the box. A fourth female finally raised her brood there.

Starlings may sometimes move their roosting site half a mile or more, but usually they exhibit an attachment for a localized area which decreases in size as the season advances. Kluijver (1935) and Schüz (1942) have noted that the males, exhibiting a stronger attachment to the nesting site than the females, range shorter distances than the females. Kluijver (1935) found that the male radius of visiting nest sites was under 100 meters before March 15, and decreased to less than 60, usually to about 30 meters, by April 1. He found that the female started with a radius of over 100 meters; and, although it decreased, it usually remained larger than that of the males.

Several times, at Ithaca, birds have been observed to alternate between roosting in the boxes at night and returning to a communal roost. One female, banded February 26, 1950, in a communal roost in the Cornell University library tower, 3 miles to the southwest of the Study Area, was found in a box on the Study Area during the night of March 20; she was in the tower again on April 7. Another female was in a box on March 20, in the communal roost on April 7, and nested on the Study Area in May. An adult male banded in a box on the Study Area on February 2, 1948, was shot on the night of February 4 in the Cornell University dairy barns, 2.5 miles from the nest box.

Sometimes a bird will roost in the same box throughout the winter season; and twice, at Ithaca, "constancy of pairing" has been observed, where both the male and the female have remained attached to the same box through two seasons. Kluijver (1935) cites one occurrence in which the same birds paired for two consecutive years.

#### ANNUAL RETURN TO NESTING AREA

When returning to an area in consecutive breeding seasons, starlings tend to choose nesting sites close to the ones they used the previous year (table 2).

In sixty-eight instances where territories of consecutive years were determined for females from 1948-51, twenty-two, or 32 per cent were found in the same nesting box as the previous year. Sixty-three, or almost 93 per cent, moved less than half a mile from their former site. Only five females were known to have moved farther than a half mile; these ranged from 1 to 2.5 miles from the nesting site of the previous year. One female used the same box for four consecutive years, and another female a box for three consecutive years; both birds raised two broods in their box at least twice. Another female, however, shifted her nesting site about a third of a mile between each of four consecutive seasons.

On the Ithaca Study Area, approximately half of the breeding females of one season returned to breed the following season. Many males likewise returned to their breeding grounds in consecutive years, but because most of the Ithaca birds were banded during the breeding season, while only females were roosting at night in the boxes, few data are available for the males. Kluijver (1935), in his studies in Holland, found that half of the males as well as half of the females returned to the area each year (table 3).

Mortality studies show that approximately half the starlings alive at the beginning of a year die during that year (see *Survival and Mortality*). A 50 per cent mortality, coupled with the fact that breeding starlings tend to return to nest within half a mile of previous nesting sites, indicates that most of the birds that do not return to the breeding grounds in successive years have died.

#### TERRITORY, COURTSHIP, AND NEST BUILDING

##### NESTING SITES AND TERRITORIES

The starling exhibits extreme adaptability in the choice of its actual nesting site, a characteristic that undoubtedly contributes to its outstanding success as a species. The starling normally chooses a hole or crevice in which to nest; a hole in a tree, in a telephone pole or fence post, under the eaves of a building, in a drain pipe, in a church cupola or barn, or even in a haystack suffices

TABLE 2.—Distances between nesting territories in two consecutive years. The Holland data are taken from Kluijver (1935); the Ithaca measurements have been converted to meters for comparisons.

Distance in meters	Females No.	(Ithaca) Per cent	Females No.	(Holland) Per cent	Males No.	(Holland) Per cent
0	22	32	5	12	7	23
1-30	6	9	4	8	5	17
31-60	5	7	3	6	5	17
61-100	2	3	7	14	1	3
101-200	5	7	11	23	1	3
201-300	8	12	18	36	11	37
301-400	9	13				
401-700	6	9				
701-1200	0	0				
1201-1600	0	0	0	0	0	0
1600+	5	7	0	0	0	0

TABLE 3.—Return of starlings to the breeding colony in consecutive years

	Breeding birds	No. birds	Returned		
			First year	Second year	Third year
Ithaca	Females Apr.-Jun. 1948	66	33	16	9
	Females Apr.-Jun. 1949	56	27	14	
	Females Apr.-Jun. 1950	64	28		
Holland	Females May 1932	61	29	15	
	Females May 1933	50	23		
	Males May 1932	52	22	13	
	Males May 1933	39	21		

equally well. Starlings have been recorded nesting in mail boxes (Wm. H. Moore, Fish and Wildlife Service Bird Distribution File), in bank swallow, *Riparia riparia*, burrows (Stoner, 1942), in crevices in sea cliffs (Ball, 1945; Godman, 1866), and in old, dome-nests of the magpie, *Pica pica*, (Andrews, 1915). In areas where other sites are unavailable, starlings will nest on the ground. Godfrey (1935) and Ticehurst (1909) have found them nesting in old rabbit holes, under loose stones along the shores, and in cracks in the ground; Harold Mathiak (*viva voce*) observed a nest at Horicon Marsh, Wisconsin, which was not more than an indentation the size of a fist in a sloping piece of ground, and nests have been found in heaps of stones (Blagg, 1893) and in old tins and boxes in rubbish heaps (Betham, 1929; Ticehurst, 1909). Starlings occasionally adapt themselves so far as to nest in the open, and not in the traditional hole or crevice. Lewis (1899), Robinson (1930), and Savage (1929) record them nesting in conifers, and Betham (1929), English (1917), and Gladstone (1910) found them nesting in dense clumps of bushes and in ivy.

The immediate vicinity of the nesting site comprises the "territory" as defined by Armstrong (1947:274): "An area defended against competing members of the same species." The territory may be limited to the hole itself (Bayne, 1933; Schantz, 1938), but Wallraff (1953) and the Ithaca studies found that it usually includes somewhat more than just the hole, perhaps a 10- to 20-inch radius about the hole.

In its choice of a nesting territory, the starling seems remarkably tolerant of other birds of the same or different species. Early in the season the expected strife and competition for available sites occurs; many a flicker (*Colaptes auratus*) or bluebird (*Sialia sialis*) has been ousted, or even killed, and many starling to starling battles have been fought at this unsettled time. Once settled in his small domain, however, the starling becomes an unobtrusive neighbor. Bodensten (1935) found a flicker and a starling nesting in the same tree with the holes only 2 feet apart. When disturbed at the nest, the two birds would fly out and sit on a branch within 2 inches of each other. Doolittle (1926) records five families of birds being raised simultaneously in a single dead maple—three starling families, one red-headed woodpecker family (*Melanerpes erythrocephalus*), and a sparrow hawk family (*Falco sparverius*). Three species

were found nesting in a single telephone pole by Cook (1934), a starling, a flicker, and a red-headed woodpecker. Kohler (1915) located a single, dead chestnut that had four old woodpecker holes in it, the distance from the top hole to the bottom being only 6 feet. A pair of sparrow hawks raised their young in the top hole, house wrens (*Troglodytes aedon*) in the hole 2 feet below, and two families of starlings in the lower two holes. Chapman (1925) "heard of five pairs of starlings nesting simultaneously in the hollow limbs of a single willow tree."

One experiment carried out at Ithaca, however, indicates that there may be a limit on how close starlings will nest, at least with members of their own species. In 1946 a colony box was erected on the side of a barn. Ten nesting boxes were combined to make a two-story colony with five compartments in each story (fig. 2). The holes were 7 inches apart, center to center laterally, and about 14 inches apart between stories. The outside measurements of the combined boxes were about 40 inches by 35 inches. This colony box was never used by more than one pair of starlings at a time. Each spring most of the compartments showed nest-building activities, but more than one nest was never completed and used at a time. It seems probable that the holes were so close together and looked so much alike that a single male claimed them all. This behavior may have been territorialism, but there may also have been an element of confusion involved. On June 1, 1946, almost every compartment had a few grasses in it; by June 5, this amount had increased to a handful. On June 16, the top story had nests that were progressively more advanced from left to right; the lower story was similar, but had eggs in the compartment farthest to the right. A similar condition existed during April and May, 1947, when a family of five young was raised in the upper left corner nest, and where progressively less nesting material occurred in the holes to the right. On May 10 the hole immediately below the active nest had one egg, which must have been laid two to eight days after the clutch in the top nest had been completed. This single egg, however, had disappeared by May 28. The young from the top nest fledged about June 1. On June 15 the bottom right corner nest had one egg in it. This egg hatched successfully but there was no further activity in any of the other compartments of the colony.

Another observation on the proximity of nesting starlings was made at Ithaca in 1946 when a nesting box was placed 10 inches beneath a hole in a telephone pole that had been occupied by a starling family the preceding year. This box was used constantly during the nesting season, but the hole in the pole was unoccupied.

The singing perch of the starling is usually some distance above the nest site and is shared with other males of the vicinity. Such places as the tops of nearby trees or roof gables make ideal song perches. On such perches males have been observed singing not 2 inches apart.

The feeding area is likewise a general territory in which all the local starlings may feed. The feeding areas may be adjacent to the nesting sites, or may be as far as  $\frac{1}{2}$  to  $\frac{3}{4}$  of a mile away.

#### SELECTION OF NEST SITE AND PAIR FORMATION

The behavior of the resident birds that roost locally in flocks during the winter and of those that roost in the nest boxes is similar during the period



of nest selection. The main difference is in the time of year that the pairs begin to stay at the nest site instead of returning to the local roost for the night.

The behavior of the box-roosting birds has been discussed previously (*Behavior During Winter*). These birds, individuals of both sexes, show an interest in the nesting sites in the fall, and continue their activities about the boxes throughout the winter, except during brief periods of unfavorable weather. Many flock-roosting birds, however, apparently do not visit the nesting sites during the winter months. Some of these birds are undoubtedly winter residents (migrants), but others appear to be residents that do not exhibit an interest in the nest sites until later in the season than their box-roosting companions. Unfortunately, the observation of these resident birds is confused by the flocks of winter residents during the winter, and by the arrival of summer residents in the spring. The fact that there was a definite increase in the number of box-roosters at Ithaca during the end of February, 1949, before migratory flocks became common (March 10), however, suggests that some of the residents do not visit the boxes until February and March.

The observations of Kluijver (1933) and Marples (1936a) appear to be of this resident, flock-roosting segment of the population. They found that some birds began visiting nesting boxes during the day, especially in the morning, during spells of warm weather in late January and early February. Usually the first birds of the season to visit the boxes from the flocks were males which would separate from a passing flock in the morning and land to sing for a short period near the nesting site. Often a solitary male visited a site, but as the season progressed small groups of males were seen singing from community song perches. At first the visits were short, some only ten minutes, and occurred only in the early morning. Later the visits became more regular and lasted longer, and evening visits became more frequent. Finally, the birds were at the nest off and on all day, except perhaps for a short period at noon. In the event of rainy, cold, or inclement weather, the visits decreased or were temporarily abandoned.

Kluijver (1933) and Marples (1936a) both found that the females did not begin to visit the boxes until as much as several weeks later than the males. When the females arrived their interest was in the nest site itself, even though it was already taken by a male. The behavior of the pair was essentially identical to that described above for the box-roosting "pairs." Kluijver noted that the behavior of the male and female differed somewhat: the female went in and out of the box a lot, while the male spent more time on the roof and less time inside.

In the course of the winter months, as previously noted, the night-roosting birds may shift their nest site many times. This is likewise true for the flock-roosters, but perhaps to a lesser extent (Kluijver, 1933). The birds usually take their time in locating the final site. The birds, especially the males, visit all the holes within a given area, singing about them and flying in and out of the holes. As the season advances the number of boxes visited decreases, and by March the male usually has a definite site selected. Schüz (1942) and Wallraff (1953) found that even after the male has chosen a hole, he often visits other boxes, especially uninhabited ones. Schüz (1942) observed that such uninhabited boxes were visited by many males from surrounding boxes, even during the breeding season.

When the male finally settles on a given nest site, he begins to discourage the intrusion of other birds, even of other species, chasing them from the immediate neighborhood of the box. During this period the fights with intruding males become quite violent. Several times fighting pairs have been seen to fall to the ground, gripping each other strongly and pecking savagely. At such times the combatants are so oblivious of their surroundings they can be approached and caught. Even when handled they will not always loosen their grip on each other immediately.

After choosing a nest site, the male will sing more continually near the site; and, if his site is a box, will spend much time on the roof. Frequently he will carry old materials out of the nest hole, and may even bring in new materials.

With the progress of the season, the female, too, becomes more attached to a given box, and the relationship between the pairs at the boxes becomes closer. Shortly, the courtship of the females by the males begins in earnest.

#### COURTSHIP AND CONDITIONS OF MATING

Courtship is not well defined in the starling. Most frequently it takes the form of intensified activities about the nesting box. Unmated males spend much of the day singing by their holes, flapping and fluttering their wings excitedly whenever another starling flies by. A male with a female already at the hole will increase his singing, doing so enthusiastically with his head thrown back, iridescent throat feathers standing out and vibrating, and wings fanning the air. At times he will pick up green leaves and carry them into the box, or he may hold them and sing as the female goes in and out of the nest hole.

A sexual chase in the starling has been reported by Bayne (1933); and Marples (1936a), Morley (1941), and Nethersole-Thompson and Musselwhite (1940) have described "branch chases" or "branch running" which may be akin to the sexual chase. Courtship displays that include posturing, bowing, bill-wiping, in addition to vigorous singing by the male, and "false preening" by the female have been recorded by May (1947) and Nethersole-Thompson and Musselwhite (1940). A behavior that suggests courtship presentations, followed by copulation, has been described by Beven (1946) and Chappell (1949).

Starlings are usually monogamous birds in that they mate as one male and one female and remain together in that relationship during the raising of a brood. A number of cases of polygyny, however, have been recorded: Eckardt (1919), Freitag (1936, 1937, 1939, 1940), Kessel (1950), Schüz (1943), and Walltraff (1953). Under these circumstances the male is usually not equally attentive to both partners, though this varies with the individual male. The male frequently aids in the incubation of both broods, but Freitag (1939) observed one male that did not help incubate either clutch of eggs. The male usually aids in the feeding, brooding, and fledging of only one of the broods, but Freitag (1937) records a male that helped care for both broods.

The status of unpaired males during the breeding season is not well understood. Greer (1929) and Marples (1936b) record single males claiming nesting sites near those of breeding pairs and being completely compatible with them. Kluijver (1933) believes, however, that many of the broken eggs,

and eggs found tossed out of active nests are due to these unmated males. He never actually saw these males engaged in such destructive activities, but he found that such wasted eggs occurred only near the boxes of unpaired males.

Observations by Allard (1940), Bierman (1944), and Schantz (1938), as well as those made at Ithaca, show that during the breeding season, and more especially when the young birds become clamorous, the boxes of the breeding birds are visited by strange starlings. The identity of these strangers is not known. They may be local birds, probably unattached, that become curious at the incessant calls of the young and the activities about the box, or they may be birds searching for nesting sites. These birds land at the opening of a box, expressing an apparent curiosity, and frequently stick their heads into the opening; rarely will they enter. If discovered by the owners of the box, the visitors are quickly pursued.

A possible explanation of some of these wandering birds may be found in observations made by Schüz (1942, 1943) and Wallraff (1953). They found that after the adult birds had begun breeding, first-year birds, mostly males, appeared in the area. These birds, singing and visiting boxes, behaved much as the adults had six to eight weeks earlier. They frequented the vicinity of breeding boxes, sometimes flying into boxes containing young, leaving quickly if one of the parents appeared. The adults, especially the females, chased the intruders away, but did not seem to take them too seriously. The first-year birds were observed visiting the boxes of noisy young most frequently. Occasionally they would carry green leaves which were dropped, and once a first-year bird was seen to carry food that was believed to have been fed to the nestlings.

Schantz (1938) tells of three unmated males which kept close company with each other until one finally claimed a nesting box and a mate and began breeding activities. The two unmated birds remained in the area all season; and on occasion, all during the season and especially after the young were hatched, they visited the box of the mated male. These unmated males would sometimes enter the box, and several times one of them came out carrying something in his bill, once a cherry pit. They behaved in much the same manner as did the visiting starlings mentioned above. Schantz also noted juvenal starlings visiting and entering the box while the nestlings were still there.

Graham (1895), Kluijver (1933), and Newstead (1908) have observed that some young are regularly fed by three birds. All three authors believed the third member of the trio to be an extra male. These trios suggest the possibility of polyandry in starlings, but there is no further evidence to substantiate this. It seems more likely that these third males were unmated birds, manifesting more intensively the visiting behavior described above.

#### NEST-BUILDING

Nest-building for the first brood is usually a leisurely affair. Frequently the male will begin cleaning out an old site and carrying in new material before he has a mate. He may bring in a quantity of green material, especially leaves, and has been recorded adding wood shavings, moss, birch bark, lichens, flowers, and other miscellaneous materials to the nest.

After a pair is established at a nest site, the nest-building continues to progress slowly and erratically. At Ithaca the first signs of nest-building appear during the third week in March, but egg-laying, on an average, does not begin until the middle of April. In this period, during the mornings and evenings of warm, sunny days, the pairs will be seen leisurely carrying nesting materials into the box. The birds, especially the male, spend much time sitting on the roof of their box with nesting materials in their beaks, sometimes dropping the material the last minute instead of carrying it into the box. During this time the female has been observed removing materials from the nest, especially those materials brought in by the male. Should unfavorable weather intervene, nest-building will be abandoned temporarily. As much as a week at a time may pass with no additions being made to the nest.

Finally, about a week or less before the time of egg-laying, nest-building commences in earnest. Both birds work industriously when at the nest, though they may be absent for long periods. The female generally carries more material to the nest than does the male. Occasionally the male will not help at all, but will just sit and sing on a perch nearby.

Some nest-building is still continued after the laying of the first egg, with occasional grasses and other materials being added until the time of hatching.

The length of time required for a starling to build a nest may be considerably shorter than the procedure described above. Many nests are built within two or three days of egg-laying; and, if necessary, a satisfactory nest can be built within a day. Wm. H. Moore (Fish and Wildlife Service Bird Distribution File) tells of a starling at Scotch Lake, New Brunswick, that attempted to nest in a mail box. She built a nest and laid an egg in it each day, the previous day's egg and nest having been removed when the mail was taken out. Occurrences of similar rapidity in nest-building have been noted at Ithaca.

In constructing its nest the starling fills the nesting cavity with grass-like materials, making a nest cup about 3 inches across and 2 or 3 inches deep toward the back of the cavity. There may or may not be a lining in the cup. McAtee (1940) records linings of feathers, red cedar bark, and leaves, but the majority of nests observed at Ithaca had no special linings.

The materials used in nest-building depend primarily on the materials in the immediate vicinity of the nests. Near barns the nests are primarily of hay; feathers may be added if poultry is near. In fields and meadows, dried grasses, straw, and weed stems are frequent components. If the nest is in the edge of a woodlot, dried leaves and their petioles, grasses, and some rootlets and vines will be used. Pine needles are utilized where abundant; one nest in a box on a white pine (*Pinus strobus*) consisted almost entirely of needles from that tree. Another nest, near a freshly cut hay field, was made completely of new-mown hay.

The nests of unmated males differ somewhat from those built by the breeding pairs. There is less material in the nests of the unpaired males than in the nests of paired birds. The material lacks any arrangement, and the nest cup is usually ill-defined. Also, as in the case of all male nests early in the season, the nests of the unpaired males contain varying amounts of such materials as green leaves and flowers.



## COPULATION

Copulation has been observed practically all year around in the starling, with the possible exception of the month of August when all sexual behavior is at a minimum. Schütz (1942) and Sopp (1932) record it in September, Freitag (1939) in December, and Morley (1941) in November and January. (Nestings, too, have been recorded in almost every month of the year—Bullough, 1942b). Beginning in March copulation occurs with increasing frequency, and it may be observed in the population throughout the breeding season.

Courtship and displays may occur preliminary to copulation. Kluijver (1933) describes a pre-copulation display in detail, and other displays terminating in copulation have been described by Chappell (1949), Freitag (1939), and May (1947). Frequently preliminary displays by the male are apparently omitted. In all observations at Ithaca, however, the action of the female in pecking the male in the neck or shoulder region was never omitted. In this act the female appears to solicit the male's attention, and it seems to serve as a "releaser" to the male who usually mounts immediately.

Sometimes a female invites a second copulation, but in the present study, she was never observed to receive it immediately. This observation is corroborated by the observations of Kluijver (1933), Schantz (1938), and Schütz (1943). Wallraff (1953) states that two matings occurring one right after another were observed rarely. Copulation has been observed to occur frequently at Ithaca while the birds are on the ground, as well as when they are on elevated places such as on roofs, tree branches, and similar sites.

## EGG-LAYING

## DATES AND FACTORS AFFECTING EGG-LAYING

The date of egg-laying in the starling varies in the different parts of North America. At Lyman, Mississippi, near the Gulf of Mexico, Burleigh (1944) records five almost fully fledged young on April 17, 1943. On the other hand, at Natashquan, Saquenay County, Labrador Peninsula, Quebec, Lewis (1935) records young fledglings on July 22, 1934. These nesting observations give approximate dates for the beginning of egg-laying for first broods of March 15 and June 15, respectively, the extremes thus far noted in North America. Between these extremes the times of egg-laying form a cline, progressing from the early dates in the south to later dates in the north (table 4). This cline of egg-laying dates parallels closely the latitudinal lines east of the 95° meridional line, the variations indicated in table 4 being caused by annual variations and by the north-south positions of the geographic locality within the latitudinal zone. With the possible exception of the more northerly nestings, these dates corroborate the generalization made by Baker (1938:578) that "As one goes north from the temperate latitudes one finds a general tendency for the egg-laying seasons of birds of all kinds to start later and later at the rate of some 20 to 30 days per 10° of latitude."

Egg-laying for second broods follows a similar, but more irregular, clinal pattern with forty to fifty days elapsing between the layings for the first and second broods. No nesting has yet been recorded south of 30° latitude; no

TABLE 4.—Dates of the laying of the first egg for the first and second broods in eastern North America\*

Degrees North Latitude	First Brood	Second Brood
30-35	Mar. 15-Apr. 5	Apr. 30-May 25
35-40	Apr. 1-Apr. 13	May 21-Jun. 1
40-45	Apr. 11-Apr. 28	Jun. 1-Jun. 20
45-48	Apr. 28-May 19	Jun. 10-Jun. 28
48-50	May 15-Jun. 7	None
Over 50	Jun. 15	None

\* Data on the time of egg-laying were summarized from material extracted from the Bird Distribution File of the Fish and Wildlife Service, U.S.D.I. In most instances the exact date of the laying of the first egg was not available, but where enough data were given on the nesting activities, the date of the first egg was back-calculated. The dates resulting from this method, while perhaps deviating as much as several days from the exact date are accurate enough for the purposes of the present study.

second broods have been recorded north of 48° latitude (Kessel, 1953).

In a given locality the majority of the starlings in a population begin egg-laying each year within three to four days of each other. This uniformity of behavior indicates that wide-spread environmental factors such as light or local climatic conditions must largely determine the time of egg-laying. Burger (1949:227) states that "photoperiodic changes are the only widely spread factor capable of modifying reproductive rhythmicity which is moderately well-known through experimental testing"; and, from available evidence for the starling he says that "photic changes are *primary* . . . agents in the external environment influencing reproductive periodicity" (Burger, 1953:238). He has shown that spermatogenesis in the starling is induced by a length of day that is sufficiently long to be stimulating, not by an increase or a decrease in day-lengths as such (Burger, 1939, 1940); and, although his recent experiments indicate that there is no "all or none" threshold, at least down to 8.5 hours, maximum gonad activation occurs at about 12.5 hours of illumination (Burger, 1953). Since spermatogenesis can take place with light intensities as low as 1.7 foot candles (Bissonnette and Wadlund, 1931), and since there is such variability in light intensities under natural conditions, Burger (1940) believes that light intensities in nature play no major role in modifying rates of spermatogenesis. He also doubts that wave-lengths are important modifying factors under natural conditions (Burger, 1940). Little is known concerning the response of female starlings to light and photoperiods, but presumably they respond in a manner similar to the male.

Although starlings in England may breed when the days are little more than 9 hours long (Marshall, 1951), under natural conditions in North America, the shortest day-length utilized for egg-laying is about 12 hours, sunrise to sunset, plus 1/3 of an hour of civil twilight (table 6). This short day-length is encountered by starlings at Lyman, Mississippi (30°30' N. Lat.), when laying begins in the middle of March. In most North American localities, however, starlings do not begin egg-laying while there are only 12 to 12.5

hours of daylight. At the time of egg-laying at Ithaca, New York, for instance, the time from sunrise to sunset exceeds 13 hours; and at Churchill, Manitoba, day-length was 16 hours and 24 minutes in 1952 when eggs were laid. Obviously other environmental factors besides light are operative.

Experimentally, Burger (1948) has shown that temperature affects spermatogenesis in the starling. Using a 14-hour day, he showed that starlings kept constantly at high temperatures of 90°F and 100°F (higher than normal at the time of spermatogenesis or egg-laying) showed greater gonad growth than did those kept at lower, fluctuating temperatures between 52°F and 72°F.

Annual variations in the time of egg-laying in a given locality appear to be due largely to temperature differences. This effect of temperature on egg-laying in the starling has been noted by Kluijver (1933) in Holland as well as in the present study. Egg-laying dates at Ithaca during the seven years of study differed as much as nineteen days, the dates of the first eggs being April 11, 1945; April 17, 1949; April 20, 1948; April 21, 1946; April 26, 1947; April 27, 1951; and April 29, 1950. At a given locality, annual differences in light at the same time each year are negligible; the day-lengths from sunrise to sunset at the time of egg-laying at Ithaca varied only from 13 hours 11 minutes to 13 hours 59 minutes during the study. Of the climatic factors studied at Ithaca, temperature is the only one that has a demonstrable effect on egg-laying. Both amount and time of heat application and the total quantity of heat seem to affect egg-laying.

Gonadal activity in the starling is at a minimum in August, but it increases slightly in mid-September and continues to increase slowly during the winter months (Bullough, 1942b; Kessel, 1951b). The effects of environmental temperatures on gonad development during the winter at Ithaca are not apparent from the present studies, the annual variations in February and even early March showing little correlation with the final egg-laying dates (table 5; compare especially 1946-1949 and 1950-1951).

Gonadal activity increases more rapidly during late February and March (Bullough, *op. cit.*; Bissonnette and Chapnick, 1930), becoming especially rapid after the middle of March. Bissonnette and Zujko (1936), for instance, cite March 25 as the beginning of the rapid growth period for the ovarian follicle at Hartford, Connecticut in 1933; and Bissonnette (1930) records a marked increase in testicular development beginning about March 19, 1927. Also, during the third week of March at Ithaca the starlings first display signs of serious nest-building. It is during this latter part of March, when gonad development is rapid, that environmental temperatures seem to have their greatest effect on the date of egg-laying. The average temperatures for the last third of March at Ithaca correlate closely with the egg-laying dates each year: When temperatures at the end of March are above an average of 40°F, egg-laying occurs markedly earlier than it does when temperatures are in the 30's (table 5).

Gonad development continues into April, the month of egg-laying at Ithaca. The environmental temperatures in April, however, do not seem to have so strong an effect on gonad development and egg-laying as those of late March (compare April temperatures in table 5 with egg-laying dates), but their influence is still manifest. As can be seen in table 5, March, 1945,

was unusually warm, and April temperatures continued high; egg-laying was unusually early. In 1946 and 1949 the late March temperatures were almost as high as those of 1945, but April temperatures were quite low; egg-laying was delayed six to ten days beyond that of 1945. The difference in dates in 1946 and 1949 appears to be the result of temperature differences after April 10.

In years when temperatures are low throughout the spring, the egg-laying dates of the starling are late. As noted above, cool temperatures in March are especially retarding to egg-laying, though coolness in April will continue

TABLE 5.—Average daily mean temperatures in degrees Fahrenheit for ten-day periods beginning at date with 10 hours between sunrise and sunset\*

	Patuxent Res. Ref., Md.†		Ithaca, New York							
	1949	1950	1945	1946	1947	1948	1949	1950	1951	
Jan. 25-29**	44.0	49.2								
Jan. 30-Feb. 8	31.3	37.6								
Feb. 2-8**			16.4	21.3	15.1	10.6	23.0	23.6	15.6	
Feb. 8**										
Feb. 9-18	42.7	39.4	26.8	26.3	25.0	25.9	32.0	31.8	24.4	
Feb. 11-18**										
Feb. 13-18**										
Feb. 17-18**										
Feb. 19-28	41.8	30.0	27.9	20.3	19.7	27.8	32.0	15.4	33.1	
Feb. 23-28**										
Mar. 1-10	37.7	32.4	32.2	38.2	26.4	22.5	29.2	19.2	30.8	
Mar. 11-20	35.5	36.0	46.6	43.6	30.9	31.0	25.4	22.9	32.9	
Mar. 21-30	54.2	45.3	50.7	48.9	31.3	42.9	49.9	36.4	36.1	
Mar. 31-Apr. 8	(47.4)††									
Mar. 31-Apr. 9		45.9	50.2	39.0	40.2	46.7	38.9	38.2	43.0	
Apr. 10-Apr. 13		(45.4)								
Apr. 10-19			(63.0)	40.6	44.7	42.2	(45.3)	40.0	42.9	
Apr. 20-29				(44.0)	(41.9)	(67.0)		43.2	(46.0)	
Apr. 30-May 9										
May 10-19										
May 20-29										
May 30-Jun. 8										
Jun. 9-Jun. 18										
Dates of Egg-Laying	Apr 8	Apr 13	Apr 11	Apr 21	Apr 26	Apr 20	Apr 17	Apr 29	Apr 27	

\* The arbitrary reference point of 10 hours between sunrise and sunset was chosen for two reasons: 1) Baker (1938), in the many birds he reviewed, found little egg-laying when days were shorter than 11 hours, and almost none when shorter than 10, and 2) while Marshall (1951) cites instances of starlings breeding with about 9 hours of daylight, Burger (1953) shows that day-lengths of 8.5 hours will induce some testicular activation in starlings, but it is not until exposed to 11 hours that testes-growth becomes regular.

† Temperature records are from Beltsville, Maryland.

‡ Temperature records are from Newberry, Michigan.

\*\* Periods do not include a full ten days.

†† Averages within parentheses include only temperatures to the date of egg-laying.



TABLE 5.—(continued)

	McMillan, Michigan†				North Bay, Ontario	Narashquan, Quebec	Havre, Montana	Camrose, Alberta	Churchill, Manitoba
	1935	1938	1941	1942	1933	1934	1943	1934	1952
Jan. 25-29**									
Jan. 30-Feb. 8									
Feb. 2-8**									
Feb. 8**	22.0	30.0	21.5	8.5	-8.0				
Feb. 9-18	22.3	18.5	21.2	19.0	7.3				
Feb. 11-18**							32.5		
Feb. 13-18**						-16.5			
Feb. 17-18**								23.2	
Feb. 19-28	13.5	17.3	16.9	17.6	24.4	5.7	30.2	9.2	
Feb. 23-28**									-18.2
Mar. 1-10	22.1	14.8	21.2	26.0	23.6	19.7	11.8	27.8	-7.3
Mar. 11-20	26.6	32.1	21.1	28.1	19.6	7.7	11.9	29.4	-3.0
Mar. 21-30	32.1	39.8	25.9	34.5	28.2	11.2	43.2	20.1	5.9
Mar. 31-Apr. 8									
Mar. 31-Apr. 9	32.9	27.5	39.2	35.5	36.2	28.6	50.5	39.8	12.9
Apr. 10-Apr. 13									
Apr. 10-19	39.7	45.8	48.5	41.9	45.0	33.2	51.0	37.4	27.0
Apr. 20-29	48.4	45.7	44.2	57.1	39.8	31.0	(49.8)	51.0	31.1
Apr. 30-May 9	(38.3)	(52.4)	(57.3)	(63.0)	(49.7)	33.2		43.2	35.0
May 10-19						35.7		53.6	
May 20-29						42.5		(48.5)	
May 30-Jun. 8						43.8			
Jun. 9-Jun. 18						(50.3)			
Dates of Egg-Laying	May 6	May 4	May 5	Apr 30	May 4	Jun. 15	Apr 28	May 23	May 9

to delay it. The effects of a cold spring can be seen by noting the cool temperatures in 1947, 1950, and 1951 in table 5 and the corresponding late dates of egg-laying; 1950 was unusually cool, the egg-laying date unusually late.

An examination of the egg-laying dates and their relationship to temperatures at Ithaca suggests that daily mean temperatures of 40 to 43°F are minimum temperatures that will reinforce light in stimulating gonad growth, at least during the latter stages of development. The threshold of effective environmental temperatures probably varies with the stage of gonadal development, but the Ithaca data are not refined enough to show such a variation. It is interesting to note, however, that in seven years egg-laying never occurred at Ithaca before daily mean temperatures had been 40°F or above for at least seventeen days (av. twenty-eight days) and had remained consistently above this temperature for at least twelve days (av. twenty-eight days). Also, the last third of March seems to be a critical period at Ithaca in the gonad growth-temperature relationship. Before this time the gonads do not seem to respond to high temperatures (compare 1946 with 1949, table 5); after this, they are stimulated.

The relationships of egg-laying to temperature at Ithaca are corroborated

by data from McMillan, Michigan; North Bay, Ontario; and Natashaquan, Quebec (table 5). McMillan and North Bay are about  $4^{\circ}$  latitude farther north than Ithaca, and mean daily temperatures do not reach  $40-43^{\circ}\text{F}$  until the middle of April. After this, however, egg-laying occurs, on the average, in twenty-five days, the specific time being correlated with the amount of heat received. For example, when temperatures at McMillan at the end of April, 1942, were warmer than usual, starlings laid earlier than in three other years for which data are available. Natashaquan is more than  $7.5^{\circ}$  latitude farther north than Ithaca, but the same temperature relationships seem to exist. In 1934 when temperatures did not reach  $40-43^{\circ}\text{F}$  until the last third of May, egg-laying began June 15. There is no "control" among these more northern examples to indicate whether or not there is a critical time before which these birds will not respond to heat stimulation.

Nesting dates recorded at the Patuxent Research Refuge, Maryland,  $2.5^{\circ}$  latitude south of Ithaca, show the same general pattern in relation to temperature as those from farther north, though the winter temperatures are considerably higher, daily mean temperatures sometimes exceeding  $40^{\circ}\text{F}$  for long periods. The fact that egg-laying does not occur until early April, in spite of warm winter weather, indicates that temperature is not an entirely effective stimulant early in the season. As at Ithaca, there is apparently a time before which temperature effects on gonad development are not pronounced. This time is undoubtedly determined by the stage of gonad development, the later stages apparently being more subject to heat stimulation than the early ones. Photoperiod is probably the limiting factor early in the season, the high winter temperatures in Maryland not being high enough or else continuous enough to counteract the short day-lengths in stimulating gametogenesis (see below). At the Patuxent Research Refuge temperatures have been higher at the date of egg-laying than at Ithaca, and more days of  $40^{\circ}\text{F}$  have elapsed before egg-laying, both phenomena probably also being related to the shorter day-lengths at the time of laying in Maryland.

Attempts were made to correlate temperatures more closely with egg-laying by utilizing the following calculations for the period between the date of 10 hours between sunrise and sunset and egg-laying: 1) Sum of degree-days above  $0^{\circ}\text{F}$  (sum of mean daily temperatures); 2) Sum of degree-days  $40^{\circ}\text{F}$  and above; 3) Total number of days with daily mean temperatures of  $40^{\circ}\text{F}$  and above; 4) The total number of days in which maximum temperatures were  $40^{\circ}\text{F}$  or above (table 6). None of these groups of data, however, taken alone, show the temperature inter-relationships satisfactorily. The main fact that is suggested by these data is that the minimum heat requirements for egg-laying in starlings are satisfied by a total of seventeen to eighteen days in which the mean temperatures are  $40^{\circ}\text{F}$  or above and which yield a sum of 110 to 150 degree-days  $40^{\circ}\text{F}$  or above. It is usually during seasons in which temperatures rise rapidly and remain high that starlings can be found breeding under these minimum heat conditions.

A comparison of the environmental temperatures at the time of egg-laying in various localities in eastern North America shows that actual temperatures at the time of egg-laying in the extreme south and in the more northerly portions of the breeding range tend to be higher than those in the intermediate

areas (table 6, av. temp. ten days before eggs). There may be several explanations for this geographic variation. First, there appears to be an inter-relationship between the length of day and the temperature at the time of ovulation. This correlation can be seen in both the total amount of light received before egg-laying as well as in the actual day-lengths at the time of egg-laying (table 6). In the South, where egg-laying occurs at short day-lengths, it is likely that the relatively high temperatures of the winter months compensate to some degree for the short days and enable egg-laying to commence early. To counteract the short days, however, higher temperatures may be required than under longer day-lengths. In the North, the winter and early spring temperatures are cooler and egg-laying does not begin until day-lengths (sunrise-sunset) are 13 or more hours. Burger (1953) found, at least below 14 hours of day-length, that the rapidity of induction of testicular activation increased with increased day-lengths; and it seems that at these longer day-lengths less heat may be required for egg-laying than at shorter day-lengths.

Another reason that laying does not occur at the same temperature at different latitudes appears to be more a function of the weather than of the starlings. It seems, at least in the years tabulated here, that once temperatures begin to rise in the North in the spring, especially north of  $46^{\circ}\text{N}$ . Lat., they usually rise rapidly. By the time temperatures are high enough to be an effective stimulant, they are increasing so rapidly that egg-laying cannot occur before they have increased into the high  $40^{\circ}$  or  $50^{\circ}\text{F}$  range.

In summary, then, day-length appears to be the primary environmental factor influencing gametogenesis in starlings, but annual variations in the time of egg-laying in any given locality are apparently caused primarily by differences in temperature, though other lesser factors undoubtedly exert influences, too. The minimum threshold for incitement of rapid gonad development appears to be about  $40$  to  $43^{\circ}\text{F}$ , and the birds must be exposed to this mean environmental temperature for a minimum of seventeen days before they will lay eggs. The important factors causing variations in egg-laying dates after exposure to minimum heat requirements appear to be 1) the pattern in which the heat occurs, i.e. consistent high temperatures, or irregular high and low temperature periods during the season, and 2) the inter-relationship of the amount of heat received and the stage of gonad development when it is received. Only controlled laboratory experiments will yield data refined enough to give more exact correlations.

A few records of egg-laying are available west of the region of  $95^{\circ}\text{W}$ . Long. and north of  $45^{\circ}\text{N}$ . Lat.: Havre, Montana ( $48^{\circ}34'$ ), Camrose, Alberta ( $50^{\circ}02'$ ), and Churchill, Manitoba ( $58^{\circ}45'$ ). Data from these localities are not in complete agreement with those from eastern North America, but too few nesting records are available for a satisfactory analysis of the discrepancies (tables 5 and 6). The localities of Havre and Camrose show temperature effects on egg-laying similar to those of eastern North America, except, in both localities, in the years for which data are available, egg-laying did not occur until thirty-four to thirty-eight days after temperatures reached the  $40$ - $43^{\circ}\text{F}$  level. This delay may be caused by the pattern of temperature increases in the spring.

The Churchill starlings appear to violate all the foregoing hypotheses. In

TABLE 6.—Comparison of egg-laying dates with latitude, day-length, total light, temperatures and total heat.

Locality	Approx. degrees N. Lat.	Date of sunrise-sunset*	Day-length (sunrise-sunset)		No. minutes at egg-laying civil twilight	Total hours light (sunrise-sunset)		Sum degree-days above 0° F.	Sum degree-days 40° F. & above	No. days daily mean 40° F. & above	No. days max. temp. 40° F. & above	No. days between consistent 40° F. daily means and egg-laying	Av. temp. 10 days† before eggs (° F.)
			Hrs.	Min.		(810.4) **	(3977) **	1099	70	75			
Lyman, Miss.‡	30.5	(Jan. 1) **	11	57	24	(810.4) **	(3977) **	1099	70	75	58.9	58.9	58.9
Nashville, Tenn.	36.2	Jan. 17	12	47	26	895.7	3692	705	53	?	60.5	57.5	60.5
Norfolk, Va.	36.9	Jan. 19	12	36	26	808.8	3668	876	61	?	57.5	57.5	57.5
Patuxent Res. Ref., Md.††	39.0	Apr. 8, 1949	12	55	27	842.9	3078	398	38	61	44	44	49.1
Chicago, Ill. Ithaca, N. Y.	41.9 42.5	Apr. 13, 1950	13	08	28	908.0	3092	334	33	67	23	23	47.1
		Apr. 5, 1933	12	53	29	739.5	2142	110	17	28	11	11	43.6
		Apr. 19, 1949	13	31	29	923.0	2796	242	29	44	31	31	44.7
		Apr. 11, 1945	13	11	29	796.5	2583	391	26	41	29	29	51.4
McMillan, Mich.‡‡	46.3	Apr. 21, 1946	13	38	30	943.9	2806	257	31	52	40	40	42.6
		Apr. 26, 1947	13	30	30	999.0	2581	139	18	40	26	26	41.8
		Apr. 20, 1948	13	35	30	916.7	2542	255	27	45	33	33	45.3
		Apr. 17, 1949	13	27	29	876.2	2597	210	25	44	28	28	44.1
		Apr. 29, 1950	13	59	31	1040.7	2636	153	17	40	12	12	43.2
		Apr. 27, 1951	13	54	30	1012.8	2909	199	27	51	31	31	45.6
		May 6, 1935	14	35	34	1070.9	2672	140	23	41	28	28	41.2
		May 4, 1938	14	30	34	1041.8	2714	261	28	39	24	24	52.4
		May 5, 1941	14	33	34	1056.4	2740	311	28	35	31	31	55.7
		Apr. 30, 1942	14	19	33	984.3	2668	261	19	39	17	17	59.1
North Bay, Ont.	46.3	Feb. 8	14	30	34	1041.8	2510	157	18	37	25	25	43.0
Nataashquan, Que.	50.2	Feb. 13	16	22	45	1667.0	3322	170	25	50	23	23	47.8
Havre, Mont.	48.6	Feb. 12	14	24	35	926.3	2677	406	40	?	38	38	51.1
Camrose, Alta.	53.0	Feb. 17	16	13	46	1267.0	3388	397	41	65	51	51	53.7
Churchill, Man.	58.8	May 23, 1934	16	13	46	1267.0	3388	397	41	65	51	51	53.7
		May 9, 1952	16	24	55	994.1	1172	16	3	15	15	0	35.0



1952 they laid about May 9, when daily mean temperatures had reached only an average of 35°F! The only explanation available at present for the behavior of the Churchill starlings is that of microclimates. In the Far North, areas exposed to the sun, particularly south-facing sites and ones protected from wind, have sharp increases in temperature compared to shaded or unprotected sites. It is entirely possible that the environmental temperatures about the buildings at Churchill (the sites utilized for nesting in 1952) averaged much higher than those used in this paper which were recorded at the airport weather station.

The foregoing discussion of factors affecting egg-laying in the starling is based on field observations. Data obtainable under such conditions are not exact, and therefore only generalized conclusions can result. Controlled laboratory experiments should be undertaken in order to understand fully the effects of environmental heat on gonad development in birds, especially the variation in thresholds and temperature effects during the various stages of gonad development, and the temperature thresholds in relation to early season temperatures and to day-length.

#### EGGS

At Ithaca, in 301 clutches laid during the entire breeding seasons of 1947, 1950, and 1951, the starling averaged 4.9 eggs per clutch. In 199 layings for the early, or "first broods" (1947, 1949, 1950, 1951), the clutches averaged 5.5 eggs. In 110 late, or "second brood" layings (1947, 1950, 1951), laid by females who successfully fledged a first brood (see Kessel, 1953), the average dropped to 4.1 eggs per clutch.

In the period between the main first brood layings and the second brood layings a few scattered clutches are laid. Forty-two such clutches at Ithaca averaged 5.0 eggs each. These "intermediate layings" seem to be mostly re-nesting attempts by females whose first nests were destroyed, for a number of banded, re-nesting females have been found in this group; the intermediate layings, however, also include some clutches of late nesters that for some reason did not lay with the early birds. Some of these late nesters at Ithaca are first-year birds breeding for the first time, a situation that Kluijver (1933, 1935) has found true also in Holland.

At Ithaca, 6 eggs is the modal number occurring in a clutch during the early laying period. The second most frequent number is 5 eggs. For northern

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\* See footnote \* in table 5.

† Temperatures were calculated for a ten-day period because Bullough (1942b) found that ten days were required in the starling for the development of a full-grown ovum after the appearance of the first yolk droplets. Also, Ithaca studies show that most starlings begin laying for re-nests or for second broods six to ten days after the destruction or completion of the preceding nest, indicating that this length of time is required for the female to produce a mature ovum (Pages 283 and 307).

‡ Temperature records are from Biloxi, Mississippi.

§ Seldom below.

\*\* Day-lengths never get as short at 10 hours. For purposes of comparison, data are calculated from January 1, giving a period comparable to other latitudes.

†† Temperature records are from Beltsville, Maryland.

‡‡ Temperature records are from Newberry, Michigan.

§§ Only briefly below.

TABLE 7.—Frequency distribution and mean clutch size of the starling\*

Clutch Size	N. England		Holland				Ithaca, New York			
	First Broods		First Broods		Second Broods		First Broods		Second Broods	
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
1			1	.06	2	1.0				
2	1	1.0	10	.6	5	2.6			8	7.3
3	7	6.7	41	2.6	28	14.5	5	2.5	19	17.3
4	29	27.6	273	17.1	80	41.4	14	7.0	39	35.5
5	47	44.8	669	42.0	64	33.2	75	37.7	42	38.2
6	12	11.4	447	28.1	10	5.2	85	42.7	2	1.8
7	6	5.7	131	8.2	4	2.1	17	8.5		1.8
8	3	2.9	17	1.1			3	1.5		
9			1	.06						
10			2	.13						
Total	105		1592		193		199		110	
Average	4.9; S.D., $\pm 1.1$		5.2; S.D., $\pm 1.0$		4.3; S.D., $\pm 1.2$		5.5; S.D., $\pm .90$		4.1; S.D., $\pm .96$	

Note: Average clutch size for May layings (intermediate broods) in Holland was 4.9, and at Ithaca, 5.0.

\* Data for England and Holland are adapted from Lack (1948a).

England, Lack (1948a) gives 5 as the modal number for the early clutches, and 4 as next; 4.9 was the mean. For Holland 5 is again the modal number, but 6 is next, giving 5.2 as the mean (Lack, 1948a).

In the second brood clutches at Ithaca, 4 eggs is modal, but 3 is a close second; 4 is the modal number in Holland (Lack 1948a).

The maximum clutch number found at Ithaca during the study was 9 eggs, and that was found only twice in six years. Eight eggs were found three times in 351 nests tabulated, always occurring in the early layings; two of these three clutches were laid by the same female in consecutive years. Kluijver (1933), in 1,804 layings in Holland, records nine clutches of 8 eggs, and four clutches of 9. He also records two clutches of 10 eggs (Lack, 1948a); and Weber (1907) records a nest of 10 eggs from the New York City region.

Table 7 gives a frequency distribution of clutch size at Ithaca and clutch sizes from similar studies by Lack (1948a) in northern England and Holland. Clutch sizes for first broods in England are significantly smaller than in Holland ( $P < 0.01$ ); and the present studies show that those at Ithaca are significantly larger than either those of England or Holland (both  $P < 0.01$ ). Data for second brood clutches are available only from Holland (June layings), and it is interesting to note that in this brood the Dutch clutches are significantly larger ( $P < 0.05$ ) than those at Ithaca.

The mean clutch size in a given area may vary from year to year. The annual variation in the clutch size for first brood at Ithaca is significant (1947, 5.5 eggs; 1949, 5.7; 1950, 5.6; 1951, 5.2); with three degrees of freedom between treatments and 198 degrees of freedom within treatments,  $F = 3.16^{**}$ . Lack (1948a), also, has shown this annual variation to be significant in the Dutch data. The reason for the variation is not known, but it may be related

to food supply (Lack, 1947-48). Creutz (1939) believes it is due to the earliness or the lateness of the season. He noted that at an early season, as 1937 in northern Germany, there are more eggs laid per clutch, that more nestings occur, and that more second broods occur. Other studies corroborate the fact that an early season is followed by more second broods; larger clutches have also been indicated. During the Ithaca studies the season varied as much as nineteen days; the number of nestings, however, remained constant (all available nesting sites were occupied), and the clutch size variation does not correspond with seasonal differences. Lack (1947-48) notes an association with the earliness or lateness of the spring, but states that this is not the major cause of clutch size variation. He does not attempt to explain the variation, however.

Attempts to prolong egg-laying and increase the number of eggs laid by a given female were unsuccessful at Ithaca. In two nests in which an egg was removed each day during laying, the female continued to lay only until her complement was completed (six in both instances), and then she began incubation. One of these had only one egg when she started incubating.

The color of the eggs of the starling vary from a light bluish-green to almost white. They have a slight gloss and are usually plain, though Witherby, *et al.*, (1943) state that eggs with fine red spots have been recorded. The eggs are ovate to elliptical-ovate in shape.

Measurements of fifty American eggs by Bent (1950) averaged 29.2 by 21.1 millimeters. The four extremes measured 31.4 by 21.4, 30.5 by 22.5, 26.9 by 20.0, and 27.9 by 19.8 millimeters. Measurements of one hundred British eggs (Witherby, *et al.*, 1943) gave an average of 30.2 by 21.2 millimeters; the maximum being 34.9 by 21.0 and 34.1 by 22.4 millimeters, and the minimum, 27.2 by 19.8 millimeters. Sixteen eggs from three clutches measured in Germany by Wallraff (1953) averaged 29.6 x 21.3 millimeters.

TABLE 8.—Egg weights (grams) at time of laying—Ithaca, N. Y., 1950  
Eggs, tabulated in sequence of laying

Nest No.	1st	2nd	3rd	4th	5th	6th	Av. Wt.
1	7.1	7.6	7.5	7.5	(7.2)*	(7.5)	7.4
2	6.3	6.3	6.3	6.6	6.8		6.5
3	7.5	8.1	7.8	7.7	8.0	7.9	7.8
4	7.2	7.5	7.3	(7.5)	(7.4)		7.4
5	6.5	6.7	6.7	6.7	6.7	6.4	6.6
6	5.9	6.9	5.8	6.0	5.8	6.0	6.1
7	6.7	7.1	?	7.0	7.0	7.0	7.0
8	5.5	6.1	6.1	6.2	5.9		6.0
9	6.9	6.9	6.9	6.8	6.8	6.7	6.8
10	7.0	7.0	7.0	7.3	7.1	6.7	7.0
11	6.3	6.3	6.3	6.6	6.4	6.3	6.4
12	?	?	7.2	7.1	7.0	7.0	7.1
13	7.5	7.2	7.3	7.1	7.0		7.2
14	6.7	6.9	7.0	7.2	7.2		7.0
15	8.5	7.8	7.9	7.9	7.4		7.9
16	7.4	7.7	7.0	7.3			7.4
All Eggs							7.0

\* Parentheses indicate sequence of laying is unknown.

Weights of eighty-five eggs of sixteen first brood clutches were determined during the 1950 breeding season at Ithaca. Most of these eggs were weighed within a few hours of the time they were laid; all were weighed within thirty-six hours of laying and before incubation began. The mean weight of the eighty-five eggs was 7.0 grams, the range extending from 5.5 to 8.5 grams. Much of the variation in the egg weights can be attributed to the tendency of some individual females to lay large eggs, and of others to lay small ones. In the sixteen clutches weighed, for instance, the mean weights of the eggs of two clutches were 7.9 and 7.8 grams, respectively, while in another two they were 6.0 and 6.1 grams (table 8). The average variation in weight between the eggs of a single clutch is 0.5 gram, the maximum variation seldom exceeding one gram. The extremes of three clutches weighed by Wallraff (1953) were 6.29 grams and 7.75 grams.

During the course of incubation there is a progressive loss in the total weight of the eggs. One clutch of six eggs lost 4.0 grams, or 9.5 per cent of its weight during incubation; another of five, lost 4.8 grams, or 12.4 per cent of its weight. These weight changes are of about the magnitude one would expect on the basis of Barth's (1953) recent work.

#### TIME AND INTERVAL OF EGG-LAYING

After the laying of the first egg, starlings continue to lay an egg a day until the clutch is completed. Only one exception was noted at Ithaca when a female failed to deposit an egg in the nest one day. It is possible, however, that this missing egg, as sometimes occurs in birds, was laid somewhere outside the nest. Kluijver (1933) cites two observations in 1,804 nests where two eggs were deposited in one day; again, however, one should not overlook the possibility of more than one female being involved. Kluijver also states that rarely a female did not lay an egg each day.

Egg-laying usually occurs during the morning hours at Ithaca, most often between 9 and 11 A.M.

After the laying of the first egg the female may spend long periods in the box. The pair tends to remain in the nesting vicinity throughout the day, and some nest-building is continued. The female may or may not spend the night in the box with the new-laid eggs. When she does spend the night in the box, she does not incubate the eggs. She may sit on the edge of the nest; or, if she sits on the nest, she does not expose her brood patch so the eggs are not warmed.

#### CLUTCH SIZE OF FEMALES IN SUCCESSIVE YEARS

The starlings tend to lay clutches of similar size each year, except perhaps in their first year when the clutch may be smaller. Lack (1948a:105), analyzing the data of H. N. Kluijver from Holland, states that the "variance between clutches of the same individual is smaller than the variance between clutches of all individuals, the difference being statistically significant at the probability of 0.01. Hence, despite some annual variation, each individual has a tendency to lay a clutch of similar size each year (after the first)." This same tendency has been noted in layings at Ithaca. Table 9, after Lack (1948a), shows successive first brood layings for females in different years,

TABLE 9.—Clutch size in successive first brood layings of the same adult female in different years

	A. In three and four successive years				B. In two successive years*	
	1	2	3	4	Holland	Ithaca
Holland (Lack, 1948a) 1932, 1933, 1934	6	6	6		3 and 6	1
	6	6	6		4 and 5	2
	6	6	6		4 and 6	2
	6	7	6		5 and 5	3
	6	7	7		5 and 6	5
	6	7	8		5 and 7	1
					6 and 6	10
	5	5(4)†	6	6(6)	6 and 7	1
	6(6)	5(4)	6(5)	5(4)	7 and 7	1
	(6)	7(7)	6(5)	6(5)	8 and 8	1
Ithaca 1948, 1949, 1950, 1951	(3)	4(2)	4(4)			
	5(2)	5(4)	6(6)			
	5(4)	5(4)	6(5)			
	(5)	5	5(3)			
	5(5)	6(5)	6(5)			
	5(5)	6	6(6)			
	6(6)	5(4)	5(3)			
	6(6)	6(6)	5(4)			
	6	7(6)	6(5)			
	(6)	7(6)	7(5)			
	7(5)	7(4)	7(6)			

\* The smaller layings did not necessarily occur in the earlier year.

† Number of young are indicated in parentheses.

tabulating both the Dutch data of Kluijver's and those from Ithaca. When combining the data of the two studies, it will be noted that only five times in seventy-seven successive layings were there annual variations in an individual's clutch size greater than one egg. About 50 per cent of the females may be expected to lay clutches of the same size as theirs of the previous season.

#### "PARASITISM" AND AVIAN NEST PARASITES

The presence of starling eggs or starling young in the nests of other birds has been reported several times. These occurrences, however, are probably accidental and not signs of parasitism in the starling. Musselman (1942) reports finding a two-thirds-grown starling in a nest with four half-grown bluebirds (*Sialia sialis*). Hoyt (1938) found a starling egg with a clutch of four pileated woodpecker eggs (*Hylatomus pileatus*); three woodpecker eggs and the one starling egg hatched, but the starling disappeared after one day. An-



drews (1915) tells of a starling egg among a clutch of seven magpie (*Pica p. pica*) eggs; and Hewett (1881) records a starling and a stock dove (*Columba o. oenas*) laying eggs in a single nest.

At Ithaca, one starling apparently laid an egg in the nest of another starling. On May 20, 1950, there were three, three-day-old young, two, two-day-old young, and one unhatched egg in a nest. The egg contained a live embryo that was only about four days incubated. Obviously this egg had been laid about the time the other clutch was ready to hatch, probably being laid by another female.

Nest parasitism on the starling by other birds has been observed several times. Blocher (1933) and Friedmann (1934) record starling nests that have been parasitized by the cowbird (*Molothrus ater*); and Bidwell (1896) lists the starling as having been parasitized by the cuckoo (*Cuculus canorus*).

#### INCUBATION

The starling usually begins incubation with the laying of the last egg. Often, however, it will begin with the next to the last egg, sometimes even with the egg before that.

Incubation is usually shared by both parents. The male and female change places frequently, with incubation periods averaging about thirty minutes. Incubation during the day may be quite irregular, and the eggs may be left uncovered for ten minutes or more at a time. Often, while incubating, the bird will leave the nest to look out of the hole, or to preen nearby for a few minutes. If not relieved by its mate after a time, the incubating bird may fly off without relief. Generally the male will not incubate as often nor for such long periods as the female, and he often jumps in and out of the nesting cavity, sometimes spending more time off than on the eggs. Wallraff (1953) found that the male's incubation time averaged only 24 per cent of that of the female's. Kluijver (1933) records several times when the male came and relieved the female, but when she flew away, he left, too.

The female is the only member of the pair that spends the night in the boxes after the breeding season has begun. She alone incubates the eggs at night, and again broods the young at night during their early development; never in the course of the present study has an exception been found. Allard (1940) in North America, Kluijver (1933) in Holland, Marples (1936a) in England, and Schüz (1942) and Wallraff (1953) in Germany have likewise found that the male does not incubate or brood at night.

With the beginning of incubation, song diminishes in the population. The males spend most of their time in the vicinity of the boxes, feeding, preening, or just sitting. Most of the song at this time seems to come from unpaired males and males that have not yet begun incubation.

Incubation has been variously reported in the literature as lasting from ten to eighteen days. At Ithaca, since incubation sometimes begins before the laying of the last egg, the length of incubation was calculated from the time of laying of the last egg to the time of its hatching. Data gathered by observations on ten such eggs during the 1950 breeding season showed, with little variation, that the eggs hatched twelve days after incubation began. The nests were visited for observation only once a day (between 10 A.M. and 12 M.), so

hatching times are not available to the exact hours. Observations on the condition of the eggs or young, however, make it possible to state that all the eggs checked at Ithaca hatched after they had been incubated from 11 days 12 hours to 12 days 3 hours.

Kluijver (1933) found the same incubation period for Dutch starlings. He states that in six boxes the last egg laid always took exactly twelve days to hatch. In 1951 the eggs of three nests observed by Wallraff (1953) took about twelve days to hatch, counting from the deposit of the last egg to the hatching of the last young. In nine other nests he records incubation as lasting from eleven to thirteen days. Schantz (1938) presents detailed data on the laying and hatching of six eggs of a clutch in Ohio. When analyzed in the light of the Ithaca studies, the incubation time of these eggs varied from 11 days 12 hours to 12 days 6 hours. The last two eggs, laid after incubation began, took about 11 days 16 hours and 11 days 19 hours, respectively, to hatch.

If the eggs fail to hatch after the normal length of incubation, the birds will continue to sit for some time. Lovell and Clay (1942) record a nest in Kentucky where incubation continued for at least twenty-two days, ten days beyond the normal hatching time; the eggs failed to hatch because of dead embryos.

Disturbances in the nesting cycle bring on varied reactions on the part of the nesting pair, the reaction depending in part on the time of the disturbances and the temperament of the bird. The removal of some of the eggs does not interrupt the cycle. Even if all the eggs are removed, if egg-laying is still underway, the cycle will continue uninterrupted. Continued disturbances by predators or human interruptions, however, as well as sudden frights, will cause desertions. Particular trouble was encountered during the present study when birds were handled at night; many would escape from the boxes after being handled and would never return. Some, however, did not seem disturbed by the handling.

If the female deserts the nest or is killed, during either egg-laying or incubation, the male will toss out the eggs within thirty-six hours or less and renew his courtship activities. Occasionally the male will continue to incubate for as much as a day before he cleans out the nest, but he has never been known to hatch the young. Sometimes a new female will arrive so quickly and begin building a new nest so soon, the eggs of the first female become buried under the new construction.

Little is known about the results of male losses. On occasion, however, the female has been noted to throw out the eggs after the male has been killed.

Several renesting attempts of females have been followed. The first egg of a renest has been found as soon as eight days after desertion of the first nest. Most renestings are found to begin within two weeks after the desertion of a previous nest, but at least one renest was recorded at Ithaca in which the first egg was laid thirty-eight days after desertion. This latter renest may have been a second attempt instead of a first.

From the data gathered at Ithaca it is not known how many times a starling will attempt to renest. Theoretically, it would be possible for them to continue renesting attempts until the middle of June. Only one renesting attempt in a

season by any given individual has been tabulated for the Ithaca Study Area, but this absence of data is no proof that more attempts do not occur. It is known that if one nesting is broken up for any reason, no second brood will be raised (Kessel, 1953).

#### PARENTAL CARE

##### HATCHING AND BROODING

At the first signs of hatching the parents show excitement and fly in and out of the nesting hole frequently. They often sit above the hole craning their necks to look inside, or sit attentively on a nearby perch. Incubation is still continued, but for the most part is more irregular and for shorter periods than previously. Occasionally parents may bring food to the nest even before the first young is hatched.

As the young free themselves from the egg shells, the parents carry the shells from the nest and drop them at varying distances from the nest site, usually about 20 yards away. Wallraff (1953) found one hatched egg shell as far as 100 meters from the nest.

The newly hatched young weigh only about 6 grams, have only scattered pre-pennae, and are completely helpless. The parents continue to sit on the nest while the young are in this condition and keep them warm. Both parents have been observed brooding during the day at Ithaca, but only the female broods at night. Allard's (1940), Schantz's (1938), and Wallraff's (1953) observations agree with those made at Ithaca, but Kluijver (1933) noted that the male did not aid in the brooding even during the day. As the nestlings develop they require less and less brooding. Wallraff (1953) found that the parents ceased brooding the young after seven or eight days.

During the first few nights after hatching, the female will cover the young. After this, however, even though she stays at the nest for several more nights, she is usually found sleeping on the edge of the nest and not brooding. Schantz (1938) found that the female he observed sometimes left the nest for periods as long as five minutes during the middle of the night. She seldom left the box itself, but stood on a perch outside, perhaps to stretch or preen.

Observations at Ithaca have shown that the female will usually stay with the young in the box at night until they are eight days old. Kluijver (1933) in Holland found that the females left after the young were five to eight days old; Schüz (1942) in Germany after nine days; Freitag (1940) in Germany after five to twelve days; and Wallraff (1953) in Germany after fourteen days. Wallraff postulates that the female leaves the young at night only when there is no longer room for her, not just until the young no longer need warmth; he bases this postulate on comparison of his and Kluijver's box sizes (13.5 x 13.5 x 31 centimeters and 13 x 13 x 35 centimeters, respectively) and on an observation by Freitag (1940) in which the nesting area was not confined and where the female remained with the nestlings from the beginning of the first brood through the departure of the second. The Ithaca observations do not add support to Wallraff's theory, however, because in spite of a box larger than either his or Kluijver's, 16 x 17 x 39 centimeters, the females stayed with the young only until they were eight days old.

#### FEEDING

Carrying food to the young does not begin suddenly. Schüz (1943) noted old birds bringing insect larvae to the nest while the eggs were still being incubated. (These larvae were not fed to the incubating partner.) As the young hatch, small bits of food are brought to the nest and fed to the nestlings that are ready to eat. The feeding of the young is again shared by both parents, the female frequently, though not always, making more foraging trips than the male. Some males do little feeding; in the late broods, or in polygynous groups, the females frequently raise the young alone.

Feeding begins about sunrise and continues to sunset while the young are small; but as they develop, feeding stops earlier, frequently as much as an hour before sundown. The most active feeding is done in the early morning and during the late afternoon and early evening hours.

The number of feedings brought to a nest each day varies considerably between nests, and there are fluctuations at the same nest on different days (Kluijver, 1933; Wallraff, 1953). In general, large broods are fed more frequently than small ones, but the difference in the number of feedings is not proportional to the number of young in the nest. Kluijver found that the number of feedings increased each day until the young were about seven days old. From seven to seventeen days of age the number of feedings a day was relatively stable, and after seventeen days the number of feedings showed a decided decrease each day. Wallraff (1953) has similar observations, the number of feedings increasing slowly during the first eleven or twelve days, increasing rapidly to a maximum at fifteen days, and then decreasing after eighteen days.

Not only does the frequency of feedings change during the development of the young, but the size of the particles fed and the manner of feeding changes. During the first few days, the parents bring in tiny mouthfuls of small caterpillars, grubs, or other insects, and carefully place them in the throats of the young. As the nestlings increase in size, larger insects are brought to them, often several in a mouthful. Feeding becomes more hurried and less careful, and the insects are quickly jabbed into the throats of the growing nestlings. By the time the young are half grown, all manner of available insect matter, including hard-shelled beetles, is fed in large mouthfuls with great rapidity. Kluijver (1933) found that during the first few days the nestlings eat about one-half their weight in food each day; by the twelfth day they consume six-sevenths of their weight in food each day.

The changes in feeding methods, as well as the tendency for the parents to feed the biggest mouth on the longest neck, makes the life of any late-hatched nestling difficult, if not impossible. Not only do these late-hatched young fail to get food, but they occasionally suffer physical damage caused by the jabs of the parent when they are fed. Several times young have been found with the esophagus and the cervical air sac apparently punctured by the parent's bill, allowing air to escape under the skin of the neck and head region and giving that region a balloon-like appearance.

#### NEST SANITATION

Defecation by the young birds begins as soon as feeding begins and occurs regularly with each feeding, especially during the first week after hatching.

Both parents aid in keeping the nest clean, although the early morning and late evening chores frequently fall to the female (Allard, 1940; Schüz, 1942). After feeding, the parent bird will often wait for the young to defecate and then, taking the excrement, which is enclosed in a fecal sac, will carefully carry it in its bill and drop it at varying distances from the nest. Allard (1940) noted that rarely the parent ate the fecal sac instead of carrying it away, but this behavior is unusual. During the early developmental period the feces are relatively solid; later they become more fluid, and the older birds, though careful, have trouble removing them. Later, too, defecation occurs more irregularly and not necessarily immediately after feeding.

During the first week the young deposit the feces in the nest cup. After about one week, however, the nestlings make an evident attempt to deposit their excrement on the edge of the nest, usually on the fore part of the nest toward the hole. Soon, if the entrance to the nest cavity is not too high, excrement will be ejected out of the hole itself. The eventual sanitation of the nest is dependent on a number of factors, including the industry of the parents, the type of food, the size of the nesting cavity, and the accessibility of the hole to the nestlings. If, as the young grow and the tempo of feeding activity increases, the parents fail to keep up with the defecation rate, or the feces become too liquid and tender for complete removal, or the cavity is too deep for the nestlings to defecate most of their excrement out of the hole, the nest will become dirty.

If the nests become excessively dirty, mortality of the young increases, and often all the young may die. The feathers of the young become wet and dirty, and the legs and feet become caked with dirt. Kluijver (1933) found that dirty nests sometimes cause the young to leave the nest prematurely at fifteen or sixteen days. It is doubtful if these young survive. Kluijver found that if the nest becomes dirty, the parents will take the dirty materials out and leave the young sitting on the bare floor of the cavity. This behavior has not been observed at Ithaca. Allard (1940) noted that the parents are continually working over the nest, poking holes into the bottom of the cup and rearranging the grasses, but he does not record the removal of dirty nesting material.

#### DESERTION OF ONE PARENT DURING THE NESTING PERIOD

Since both parents assist in the incubation and fledging of the young, one would expect that either member of the pair, should the other disappear, would care for the family. This, however, is not always the case. If the male disappears, the female usually continues raising the family. This circumstance, as mentioned above, is encountered fairly regularly in the late broods and in polygynous associations. In the reverse situation, however, where the female deserts the nest, the male rarely continues caring for the young. Since the female is the only member of the pair that broods at night, the success of the brood of a lone male during the early days would be rare. But even after this critical period, the desertion of the female almost invariably means the death of the young. This failure of the male to continue raising the young at Ithaca has been observed on numerous occasions when the female deserted because of being handled at night. Only once was a male known to raise the young alone. This one time occurred in 1948 and is especially interesting



because the female deserted when the young had just hatched. The female was seen about the vicinity of her box for a day after she deserted, but she was never seen to enter the box. The male, however, fed the young regularly, and he probably brooded them during the first days. It is improbable that the male brooded the young at night, but the female deserted on May 25 and the nights were warm enough to allow the nestlings to survive.

Freitag (1936) records a rare instance in which a male raised the second brood alone.

Marples (1936a) tells of a male that undertook the feeding activities at a box alone for one day. Two young had already left the nest and the female was caring for them on the lawn; the male cared for the young that remained in the box for an additional day.

## YOUNG

### NUMBER OF YOUNG

Brood size as well as clutch size varies in the starling. At Ithaca, during the entire breeding seasons of 1947, 1948, 1950, and 1951, the average brood size was 3.9 young in 304 broods studied, one less than the average clutch size for the entire season. The extremes of brood size at Ithaca ranged from nests of 1 young to one nest of 8 young. Two broods of 9 young and one of 10 have been recorded in Switzerland (Lack, 1948a).

In 230 broods hatched from the main first brood layings (1947-1951), the average brood size was 4.5 young. In 41 broods hatched from the intermediate layings (1947, 1948, 1950, 1951) the average size was 3.5. In 78 second brood hatches (1947, 1948, 1950, 1951), the mean brood size was only 2.9. Five was the modal number found at Ithaca in the first broods, with 4 a close second. In the intermediate layings 4 was the modal brood number, and in the second brood the modal number was 3.

Table 10 tabulates the frequency distribution of brood sizes found at Ithaca and those found in various European studies. The Ithaca data have been adapted by tabulating the first broods under "Early Broods," and the intermediate and second broods together under "Late Broods," so that they are comparable to the other works summarized in the tables.

Brood sizes from England and those of the Continent (Holland and Switzerland) were found to be significantly different by Lack (1948a), the English starlings averaging somewhat smaller broods. The early (first) broods at Ithaca are not significantly different from those of Holland or Switzerland, but the late broods are significantly smaller ( $P < 0.01$ ).

Since data are available both for clutch size in first and second brood layings and for brood size for early and late broods in Holland, these European data have been selected for comparison with the Ithaca data. It will be remembered that the first brood clutches in Holland were significantly smaller than at Ithaca, New York; Holland having an average clutch size of 5.2 (S.D.,  $\pm 1.0$ ) and Ithaca one of 5.5 (S.D.,  $\pm 0.9$ ) (table 7). It is interesting, therefore, to note that the brood size of the early nestings are almost identical: Dutch brood sizes average 4.4 (S.D.,  $\pm 1.3$ ), and Ithaca broods average 4.5 (S.D.,  $\pm 1.3$ ). These data indicate that the Ithaca starlings have a higher nest mortality than the Dutch birds. This differential mortality is again seen,

TABLE 10.—Frequency distribution and mean brood size in the starling.\*

Brood Size	N.W. England		Holland		Switzerland		N. Germany		Helgoland		Ithaca, N.Y.	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
<i>Early broods, or first broods (young in May)</i>												
1			30	2.2	65	1.8	1	2.0			8	3.5
2	66	7.2	98	7.1	164	4.7	1	2.0			9	3.9
3	166	18.2	189	13.7	426	12.1	5	10.2	11	13.4	30	13.0
4	311	34.1	395	28.9	989	28.1	12	24.5	26	31.7	63	27.4
5	295	32.3	425	30.9	1235	35.1	24	49.0	32	39.0	66	28.7
6	69	7.6	196	14.2	526	15.0	5	10.2	12	14.6	49	21.3
7	6	.7	41	3.0	93	2.6	1	2.0	1	1.2	4	1.7
8			3	.2	15	.4					1	.4
9					2	.06						
10					1	.04						
Total	913		1377		3516		49		82		230	
Average	4.2		4.4		4.5		4.6		4.6		4.5	

	N.W. England			Holland		Switzerland		N. Germany		Ithaca, N.Y.		Ithaca, N.Y.		
	Late broods (young in June and July)								Second Brood †					
1				34	5.5	44	3.8	1	2.9	11	9.2	7	9.0	
2	31	17.0		77	12.5	96	8.3	5	14.7	28	23.5	23	29.5	
3	66	36.1		145	23.5	254	22.1	19	55.9	34	28.6	24	30.8	
4	57	31.1		194	31.4	391	34.0	7	20.6	32	26.9	19	24.4	
5	25	13.7		124	20.1	285	24.8	2	5.9	13	10.9	5	6.3	
6		4	2.2	29	4.7	73	6.3			1	.8			
7				14	2.3	7	.6							
Total	183			617		1150		34		119		78		
Average	3.5			3.7		4.0		3.1		3.1		2.9		

\* Data for England, Holland, and Switzerland adapted from Lack (1948a); for N. Germany from Creutz (1939); and for Helgoland from Berndt (1939).

† Average size for 711 second broods (late June and July) in Switzerland was 3.7; for 11 second broods in Helgoland was 3.8.

though not so clearly, in the late broods. Here it will be recalled that Holland had a mean clutch size of 4.3 (S.D.,  $\pm 1.2$ ) for second brood layings, and Ithaca one of 4.1 (S.D.,  $\pm 0.96$ ). In brood size, however, Holland has an average of 3.7 young (S.D.,  $\pm 1.4$ ), and Ithaca has an average of only 3.1 (S.D.,  $\pm 1.2$ ), a difference that gives Ithaca a significantly lower brood size than Holland for the late nestings.

The greater mortality of Ithaca starlings as compared with the Dutch starlings is indicated also in the per cent of eggs that produce young that fledge. Lack (1948a) records an egg-to-fledgling success of 83 per cent in the early broods, while at Ithaca this success is 81 per cent (see *Nesting Success*). Lack records 78 per cent of the eggs of the late broods producing young that fledge, while at Ithaca the per cent is only 68.

The reasons for these mortality differences are not known. Why Ithaca

TABLE 11.—Number and per cent of young fledged for various sizes at Ithaca, 1947-1951; nestings that were total failures are excluded

Clutch Size	First Brood					Intermediate and Second Broods				
	Number clutches	Total No. Eggs	No. Young fledged	Av. No. fledged per clutch	Per cent fledged	Number clutches	Total No. Eggs	No. Young fledged	Av. No. fledged per clutch	Per cent fledged
1										
2	1	2	2	2.0	100	6	12	12	2.0	100
3	6	18	16	2.7	89	11	33	25	2.3	76
4	14	56	48	3.4	86	20	80	49	2.4	61
5	63	315	250	4.0	79	41	205	137	3.4	67
6	69	414	353	5.1	85	13	78	48	3.7	62
7	16	112	85	4.7	67	1	7	6	6.0	86
8	2	16	9	4.5	56					

starlings should lay more eggs than the Continental birds for the first brood but fewer for the second, and why the Ithaca ones should have a lower fledging success for both broods remains a puzzle at present. The answer may lie in the hypothesis developed by Lack (1947-48:319, 1948a) that the "average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region . . . natural selection eliminates a disproportionately large number of young in those clutches which are higher than average, through the inability of the parents to get enough food for their young . . ." It might be that the Ithaca starlings, perhaps still not perfectly adjusted to their relatively new environment, produce clutches above the optimum size and are unable to raise so many, but there are no data from Ithaca to substantiate this premise. Nesting success in relation to clutch size at Ithaca is shown in table 11; and, while the decreased nest success in first broods with clutches over six is suggested, the data are too few to be significant. Lack (1946a, 1948a, 1949), in several small passerines, including the starling,

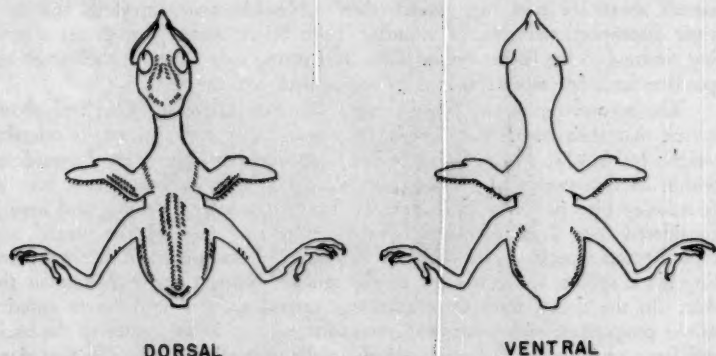


Fig. 4.—Distribution of pre-pennae on newly-hatched starlings.  
(Drawing by P. N. Adams.)

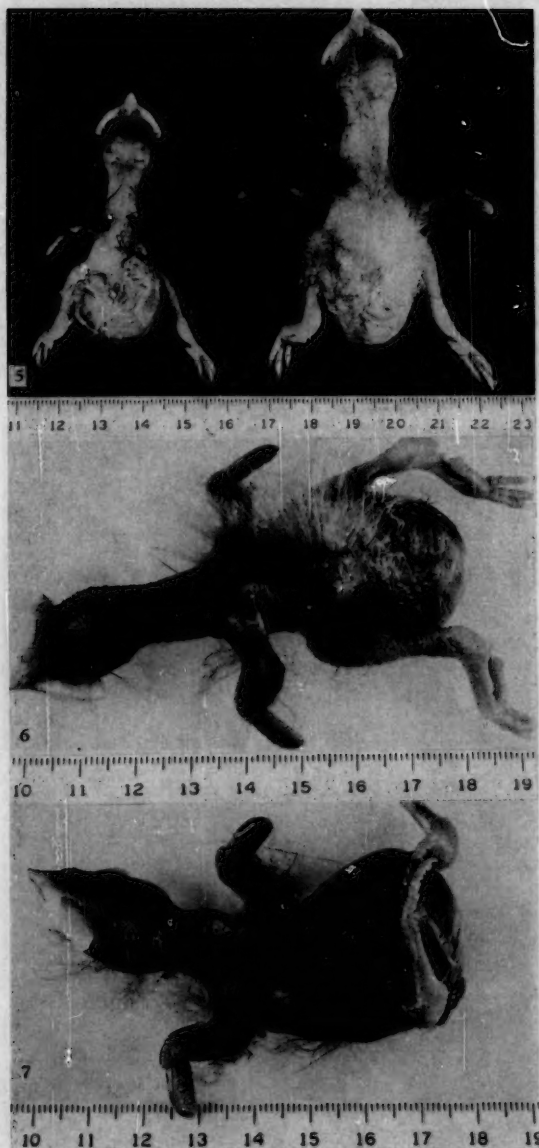
found that differential mortality did not become evident until after the young had left the nest, but sufficient data on post-fledging mortality in relation to brood size at Ithaca are not available. After leaving the nest, however, the mortality rates for the first year of life in North American starlings appear to be somewhat lower (about 60 per cent) than in the Continental birds (Switzerland=73 per cent) (see *Survival and Mortality*).

#### GROWTH AND DEVELOPMENT

The nestlings at hatching are helpless and naked, except for sparse tracts of pre-pennae (figs. 4 and 5). The pre-pennae occur in rows one or two feathers wide and do not indicate the extent of the definitive feather tracts. The only feathers on the ventral surface are those in the posterior region of the future ventral tract; these ventral pre-pennae are only 2 to 5 millimeters long, the longest occurring posteriorly. There are two tracts in the capital region: one begins at the dorsal, posterior edge of the eye and circles around the occipital region where it meets the tract from the other side; the other, a short paired tract, lies medially to the anterior end of the first. The pre-pennae in the capital region vary from 8 to 13 millimeters in length. There are no cervical feathers, the dorsal feathers beginning in the region of the pectoral girdle and extending posteriorly in a band two to five feathers wide to the uropygial gland. The dorsal tract supports the longest pre-pennae, some being 12 to 18 millimeters long in the center portion of the back. The scapular region has a single row of feathers growing up to 15 millimeters in length, and the femoral tract supports two rows with feathers up to 13 millimeters in length. There is no sign of the crural tract. The alar region supports a double row of pre-pennae on the ulna, about seven feathers in length. In the region where the future remiges and rectrices will grow, small projections, suggestive of fine hairs, barely project through the skin. These projections seem to have no relation to the final feathers that grow here, even though they occur at the same spots.

The young are hatched with their eyes closed, and when any movement occurs about the nest they stretch their rubber-like necks upwards and open their disproportionately large mouths. Their bright orange throats are a striking contrast to the lemon-yellow bills. The young may maintain their stretched position for a few seconds before collapsing back into the nest.

The second-day young appear identical to the first-day described above, except that their bodies have grown in size and they have gained considerable weight (table 13). [N.B. When a bird is aged as one day old, it is considered within its first twenty-four hours after hatching, or in its first day of life. A fourth-day bird is a bird that is in its fourth day after hatching, and here is considered four days old. Etc.] On the third day (fig. 5) the ventral and capital tracts remain unchanged; but in the dorsal, scapular, and femoral tracts tiny black specks, the first signs of the contour feathers, are visible under the skin. In the dorsal tract these markings extend about 8 millimeters anterior to the pre-pennae, widen into a diamond-shaped area in the center of the back, and form an inverted Y-shaped area about the uropygial gland. The first signs of the primaries and secondaries can also be discerned as tiny black spots on the tract.



Figs. 5-7.—5. Nestlings one and three days old, respectively. Note the rapid size increase. 6. Dorsal aspect of a four-day-old nestling. 7. Ventral aspect of a four-day-old nestling.



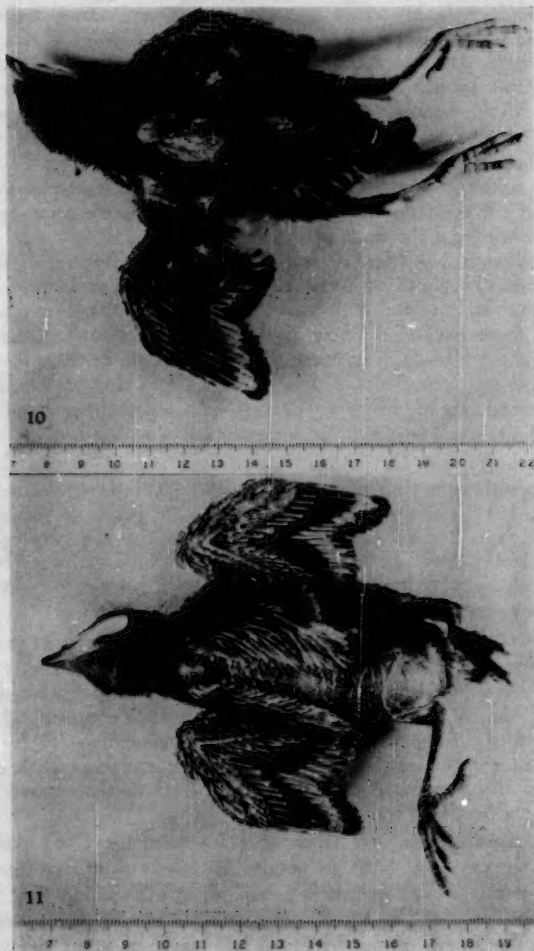
By the fourth day the nestlings have about quadrupled their hatching weights (table 13; figs. 6 and 7). They support this weight on their round, protuberant bellies; and they crawl about vigorously, using their wings and legs to propel themselves. Signs of the contour feathers have extended, the ventral tract showing black spots throughout, even to the hyoid region. The breast region is the most heavily spotted. The capital tract also shows black spotting in the center of the crown region, and scattered spots occur over the tibia for the first time. The femoral tract has darkened in aspect, as likewise has the scapular tract which is now extending ventrally to meet the anterior part of the ventral tract. The back of the neck begins to show some specks, and the rest of the dorsal tract is as described under the third day, but much darker. On the alar tract, the remiges have become very dark. The primary greater coverts are discernible, as are all the secondary coverts and the alula.

The evidence of the definitive feathers continues to extend and darken as described above, until finally, on the sixth and seventh day, a few sheaths begin to break through the surface of the skin (fig. 8). At this time the ventral



Figs. 8-9.—8. Seven and a half-day-old nestling.  
9. Nine and a half-day-old nestling.

tract in the head region has extended laterally around the quadrate region and has met the lateral extensions of the capital tract. The chin shows its first inconspicuous black dots. The sheaths of the anterior, lateral portion of the ventral tract and of a small area of the dorsal tract just anterior to the uropygial gland begin to break the skin. Some scattered feathers on the body between the main tracts are barely breaking through the skin. During this period, too, the sheaths of the alar tract begin to break through. The inner-



Figs. 10-11.—Eleven-day-old nestling. 10. Dorsal aspect. 11. Ventral aspect.

most primary and the innermost secondary push through at about the same time, and the alula follows shortly. The most anterior of the alular feathers comes in first, then the middle one, and finally the posterior one; they all break the skin within a day of each other.

The eyes open on the sixth or seventh day, also. Advanced nestlings may have their eyes open on the sixth day, but most open on the seventh. A few fail to open until the eighth day. After the eyes open, the birds no longer respond to movements of the nest with stretched necks, open mouths, and food calls. Instead, they huddle down into the nest cup and remain quiet. When handled, however, they show no real fear and do not attempt to escape.

By the eighth day the posterior region of the ventral tract is beginning to show the feather sheaths and feather tips projecting from under the skin, and the sheaths of the femoral and scapular tracts are projecting. The remiges have increased in length (table 12), and the sheaths of the rectrices have begun to show.

By the tenth day the remiges and rectrices have broken out of the sheaths (fig. 9); and the ventral tract is becoming brown from the many feather tips that have broken from the sheaths.

By the eleventh day (figs. 10 and 11) the belated feathers in the frontal region of the head begin to push their sheaths through the skin; and the feathers in the occipital and parietal regions are pushing out of the sheaths. By the twelfth day three rows of feathers in the ventral tract can be seen growing medially to those already present on each side. These feathers have sheaths that never project from the skin, but at twelve days the feathers themselves are 3 millimeters out of the skin. Twelve days is also the average time that nestlings begin to show fear and attempt to escape when handled.

Most of the feathers in the head region are feathering out of the sheaths by the fourteenth day, with only the chin and upper throat feathers still in sheaths (fig. 12). The posterior region of the chin begins to feather out on the fifteenth day. Beginning about the fourteenth day the nestlings become quite active in the nest. They stretch and beat their wings in the boxes, and are often seen with their heads out the entrance holes, especially when a parent comes to feed.

From the fifteenth day until the young leave the nest at twenty-one days, the body, wing, and tail feathers continue to develop (fig. 13). At the time they finally leave the nest the young are almost as fully feathered as their parents, and can fly well. Some nestlings are capable of sustained flight by the nineteenth day after hatching, but others at this time can fly only 15 to 20 feet. At the time of fledging the young may still retain their egg-tooth; and some of the pre-pennae may still be attached to the contour feathers, especially in the head and rump region.

Various measurements were taken of a few nestlings (1-5) during their developmental period in 1950 to obtain an index to growth (table 12). The rate of plumage development is so regular in the starlings that it can be used as an indicator of the age of the nestlings. During the present study, for instance, the growth of the first secondary was used as an indicator. The sheath of this feather breaks through the skin about six and a half to seven days after hatching. The sheath increases in length each day, and on the



Figs. 12-13.—12. Fourteen-day-old nestling.  
13. Eighteen-day-old nestling.

ninth day the feather begins to break out from the distal tip of the sheath (fig. 9). The remiges continue to grow steadily at the rate of approximately 4.5 millimeters a day until about the twentieth day. Either the total length of the secondary or the length of the feather projecting beyond the sheath can be used as an indicative measurement for aging the nestlings (table 12). The wing feathers are accurate age indicators up to at least fifteen days, but

TABLE 12.—Measurements (in millimeters) of developing nestling starlings at Ithaca, New York. First brood 1950

Age in Days	Length of Sheath of 1st Secondary	Length Feather Projecting from Sheath	Total Length	Length of Sheath of Central Tail Feather	Length Feather Projecting from Sheath	Total Length	Total Length of First Alula	Culmen	Tarsus	"Hand"	"Forearm"	Flattened Wing
1								8	9	9.5	9	
2								8	11	10	10.5	
3								10	12.5	10	13	
4												
5												
6.5	3											
7	2-3		2-3					14	25	22	25	
8	6-7		6-7					14	27	22	30	
9	9-10	1	10	2		2	3					
10	18	2.5	20		(2)	(2,5.4)	(7)					
11	17	6	23-24	6	0.5-3	(5-7)	(10)					
12	19	10-15	26-29	6.5	6	9	13	17	29			
13	20	13-18	35-38	8	9	12.5	16.5	17.5	30	33	35	
14	17	22-24	41-43	9	11	17	22	18				
15	15	29-35	44	9	12-13	20	23.5	19	30	33	35	
16		(33-37)*	(48-52)		(17)	21	25	20				
17		(40-44)	(53)		20	(25-33)	(26)					
18	10	(45-47)	55	9	21-28	(34-35)	(27)	20.5	33			95
19	9	48-50	57-58	9	30	36	28	21				95-102
20	10	52-57	60-62	10	31-34	39	29	21				101-103
21	6	54-57	60	11	32-35	42	30	21				103-109
22	0	60-63	60-63	7-11	34-42	46	31	22				
23	0	63	63	9	40	45-49	29-32	22-23				106
						49	32	22				

\* Parentheses indicate estimated measurements.



after this their growth is too variable to be reliable. The length of the central rectrices can then be used. They break out as sheaths on the eighth day, and the feathers break out of the sheaths about the tenth day (fig. 9). The tail feathers continue to grow until the starlings fledge (table 12).

The results of the current study seem to differ little from the growth and developmental studies of the starling by Portmann (1938) and Warga (1938); comparisons, however, are difficult because of differences in age terminology and in the measurements taken.

#### WEIGHTS OF NESTLINGS

An intensive study was made at Ithaca in 1950 of the natural weight increases in nestling starlings. Regular weighings were made during the developmental period of forty nestlings in eleven first broods and twenty-three nestlings in eight second broods.

A gram-balance was carried into the field, and the weighings were made at the nest boxes. The balance was set up in the car where it was protected from the wind, and the nestlings were brought the short distance from the box to the car, a brood at a time, for weighing. Each bird was weighed individually. When they first hatched, a colored thread was tied loosely about the tarsus for individual identification; later, when the birds were large enough, a permanent, size 2, Fish and Wildlife Service aluminum band was put on the leg. The birds were weighed as close to the same time each day as possible, between 10:30 A.M. and 12:30 P.M. Since the young hatch at any hour during the day or night, they were not all exactly the same age when weighed. A nestling, for instance, may have been twelve or six hours old, or just hatched at the time of its first weighing, but, for the purposes of this study, it is still classified as a first-day bird. The irregularity of hatching time accounts in large part for the variations in weights shown in table 13, especially in the first three or four days of first brood nestlings.

The increase in weight of first brood nestling starlings is rapid and somewhat sigmoid in form for the first ten to twelve days after hatching, at which time the young approach the weight of the adult bird, sometimes even exceeding the weight of their parents (fig. 14A). In the first brood, when conditions are apparently optimum for growth and the activities connected with it, there is little variation in the weights of nestlings, especially during the first three or four days. During the early period, in normally healthy nests, weight is constant enough so that birds can be aged by their weights with a fair degree of accuracy (table 13).

After ten to twelve days the weight curves begin to level off and to fluctuate somewhat (fig. 14A); this age corresponds to the time the plumage begins rapid development, energy apparently now being utilized primarily for plumage development instead of body increases. Maximum weight is usually attained between the fourteenth and eighteenth day; after this time the young may or may not lose weight before leaving the nest. The nestlings of the first brood usually lose weight before fledging, sometimes up to 16 grams each, but those from the second brood usually do not (table 13).

The weights of the second broods are not as constant as those of the first broods. Although the weights are the same as the first broods at hatching, the gains are slower and there is considerable individual variation. These

TABLE 13.—Weights, in grams, of developing nestling starlings under natural conditions during 1950 at Ithaca, New York, excluding any young in a given nest not hatched on the first day

Age in Days	First Brood				Second Brood			
	No. Speci- mens	Mean	S.D.	Maximum Minimum	No. Speci- mens	Mean	S.D.	Maximum Minimum
1	39	6.4	9(.9)*	8.5	17	6.5	1.2	8.5
2	40	10.0	1.1(1.2)	12.7	14	8.5	2.1	13.5
3	40	14.9	2.1	18.5	13	12.5	3.0	18.5
4	21	21.2	1.9	23.5	21	18.1	4.4	25.4
5	27	28.3	4.2	34.5	12	20.6	4.4	28.3
6	29	34.5	4.1	45.4	16	29.1	6.0	39.2
7	16	46.5	2.9(5.1)	51.0	11	38.4	4.2	44.4
8	27	50.3	3.1	64.7	10	39.2	9.0	54.5
9	21	57.9	3.2	64.5	16	42.9	9.0	58.2
10	33	64.4	3.7	73.0	5	55.3	4.2	62.3
11	15	71.4	2.3	74.1	12	50.4	8.5	61.7
12	19	71.0	4.9	83.0	8	57.6	8.2	69.0
13	20	71.9		80.5	11	55.3		68.0
14	16	77.1		81.5	8	61.4		68.9
15	18	75.7		87.8	7	54.9		66.7
16	8	75.3		80.3	8	63.7		73.2
17	18	78.0		88.2	3	69.2		72.7
18	8	78.8		85.3	8	66.8		73.1
19	17	74.4		85.8	3	63.6		64.6
20	18	71.3		81.2	7	67.6		72.8
21	24	71.2		80.0	—	—		—
22	20	70.9		79.2	4	67.9		70.8
				64.5				64.0

\* Parentheses under "Minimum" indicate an abnormally low value found; and parentheses under "S.D." show standard deviations including this one low value, and the other "S.D." value excludes it.

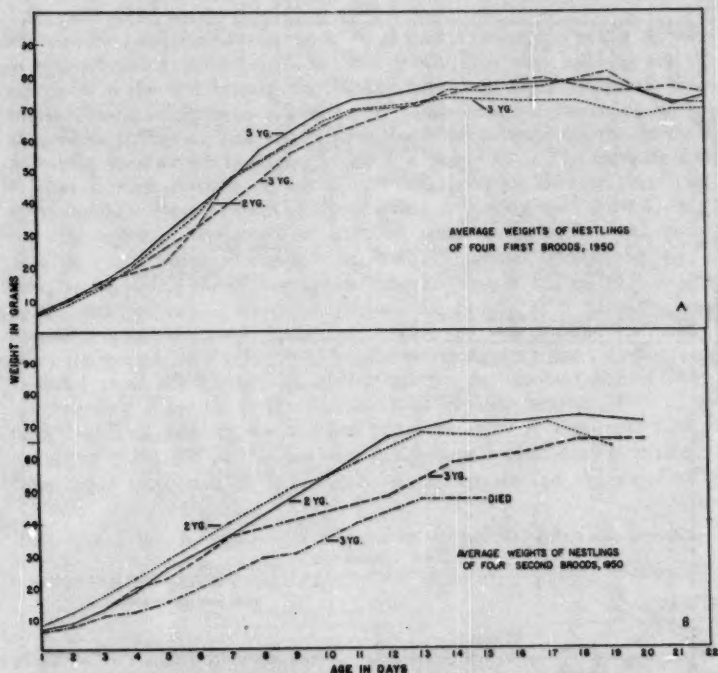


Fig. 14.—Growth curves showing the average weights of the nestlings for each nest. The averages exclude all late-hatched young and early deaths. A. Four first broods; B, Four second broods.

changes in the second brood weight gains are apparently due, at least partially, to the waning industry of the parents in bringing food to the young, the males sometimes being absent entirely; to the presence of nest parasites, which are essentially lacking during the first brood; to increased temperatures; and probably to the reduced availability of food. The weight curves of the second brood nestlings frequently do not begin to level off until twelve to fourteen days or later (fig. 14B). The maximum growth realized by individuals of the second brood is rarely as great as that of the first broods, the young of the second brood averaging lighter even at the time of fledging.

As mentioned earlier, any young that hatch a day or more later than the others of the nest are definitely handicapped. Growth is so rapid during the first days that any bird with a day's disadvantage frequently has difficulty in getting food. Sometimes, if the competition is too keen, a late hatched young will shrivel up from starvation and die, as diagrammed in fig. 15A. At other times it may survive, but never catch up to its companions in weight (fig. 15A). Then again, after a varying length of time, the late-hatched may catch up to, and sometimes overtake, the rest of the nestlings in the box (fig. 15B).

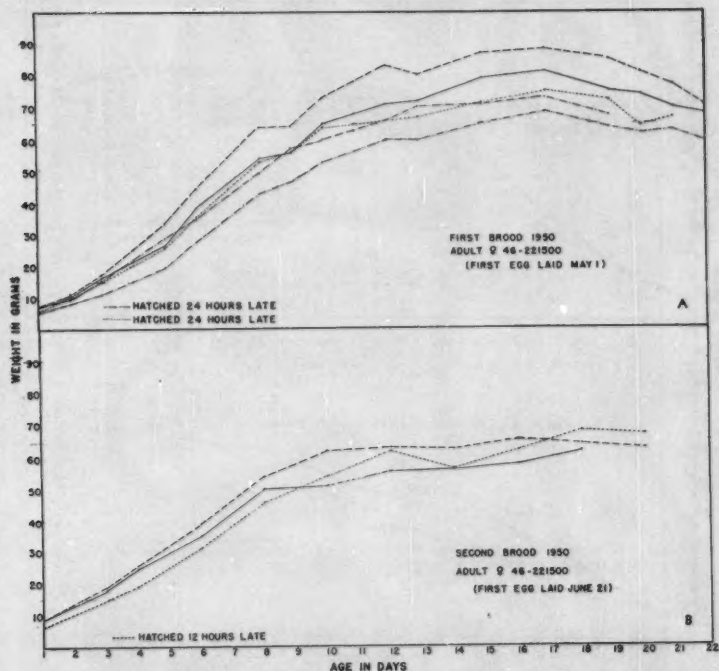


Fig. 15.—Growth curves of the individual nestling. A. First brood of an adult female; B. Second brood of an adult female.

Figs. 15A and 16A and figs. 15B and 16B chart the growth of individual nestlings in two first and two second broods, respectively. Here a complete picture of each brood is shown, with all nestlings represented regardless of the time of hatching. These charts emphasize the fact that essentially all nestlings exhibit similar growth curves, even though there are individual variations in the actual weights. The amount of weight variation within a single brood varies between different broods. As seen from fig. 16A, in some nests the young all weigh essentially the same and gain at the same rate. In other nests, however, there may be as much as 20 to 25 grams difference in the nestlings at a given age (fig. 15A), especially after they have reached the leveling-off point. Second broods show greater individual variations within a brood more consistently than do the first broods.

Lack and Silva (1949), Gibb (1950), and Lees (1949) also have found marked individual variations in the weight of the nestlings of several passerine species, and Gibb (1950) found that nestling weights in tits (*Parus major* and *P. caeruleus*) tended to decrease as brood size increased, especially in years when food was scarce. Lack (1948a) presents a few data that suggest this same trend of weight variation in starling broods, and additional data

are available from the Ithaca studies. As indicated earlier, the weight differences of Ithaca nestlings during the first three or four days after hatching are small, especially in the first brood, and are due largely to slight differences in age, certainly not to differences in brood size. Later, however, variability increases, and, when correlated with brood sizes, tends to substantiate the concept of decreasing weight with increasing brood size (table 14). The tentative nature of the correlations must be borne in mind, however, because there are so many variable factors—individual variations in young and parents, age of parents, degree of uniformity of hatching times within each brood, etc.

One might expect the broods of first-year females, nesting for the first time, to be poorer than those of adult birds. Such a difference is suggested in the one instance in which weights of the broods of a first-year female, banded as a nestling, were obtained. Figs. 15A and 15B and figs. 16A and 16B chart the growth of the first and second brood nestlings for an adult female (banded as an adult April 28, 1948) and for the first-year female (banded as a nestling May 23, 1949) for the 1950 breeding season. Both of these birds laid their first egg for the first brood on May 1, 1950, and both laid six eggs. (One egg of the first-year female was broken during incubation.) Both began incubation on May 5, the day before the last egg was laid; and

TABLE 14.—Average weights in grams of nestlings for various size broods.  
First broods, 1950\*

Brood Size	Age of Female Parent†	Av. Wt. at Max. Wt.		Age of Max. Wt. (Days)	Av. Wt. at 21 Days	
		Individual Broods	Combined Broods‡		Individual Broods	Combined Broods‡
2	ad	83.4	82.4	18	74.6	73.7
2	ad	81.4		18	72.7	
3	"1st-yr"	79.7	(79.7)	17	73.4	(73.4)
4 <sup>x</sup> , ††	"ad"	80.1	77.8	17	76.1	70.4
4 <sup>**</sup> , ††	"ad"	79.5		18	67.2	
4 <sup>x</sup> , ††	"ad"	73.7		14	68.0	
5††	ad	78.9	78.1	17	71.8	70.7
5‡‡	ad	77.3		17	69.6	
5 <sup>x</sup> , <sup>x</sup> <sup>x</sup>	1st-yr	71.6		17	65.7	(69.0)

\* Any young disappearing by the fifth day are deducted from brood size; young hatching a day later than the rest of the brood are included in the weight averages.

† Quotation marks about age of female parent indicate age determination by hackle feathers (see Kessel, 1951a); others banded in previous years and are known to have bred previously.

‡ Parentheses indicate that a brood raised by a first-year female is included in average.

<sup>x</sup> Averages include one nestling a day younger than the rest of brood.

<sup>\*\*</sup> Averages include two nestlings a day younger than the rest of brood.

†† Brood growth curve charted, without late-hatched individuals, in fig. 14A.

‡‡ Individual growth curves charted in fig. 15A.

<sup>x</sup><sup>x</sup> Individual growth curves charted in fig. 16A.



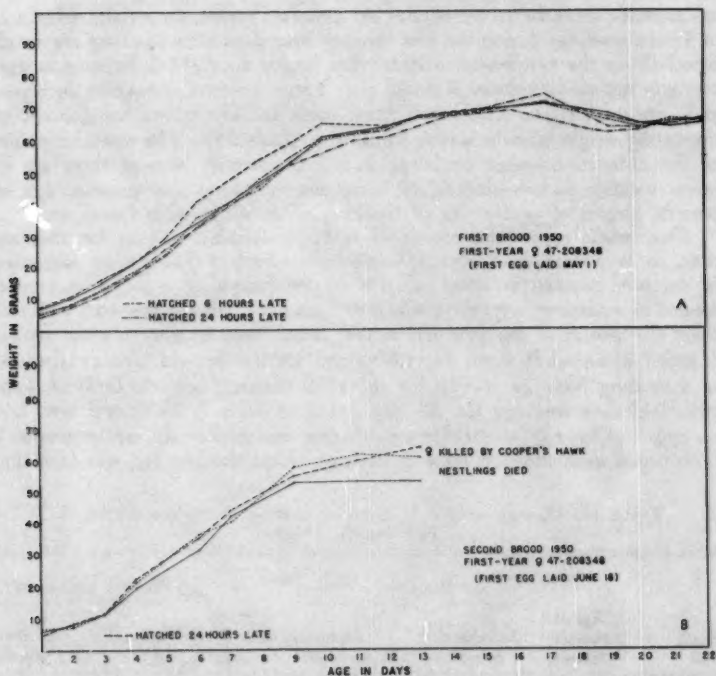


Fig. 16.—Growth curves of the individual nestlings. A. First brood of a first-year female; B. Second brood of a first-year female.

both hatched all but one egg on May 17, leaving one each to hatch on May 18. For the second brood, the adult female laid three eggs, the first being deposited on June 21. Incubation began on June 22, again a day before the last egg was laid. Two nestlings hatched on July 4, one on July 5. The first-year female laid four eggs, the first one on June 18. She also began incubating a day before the last egg was laid; and three young hatched on July 2, and the last on July 3.

These two females apparently raised their broods under almost identical environmental conditions. A comparison of the weight gains of the nestlings of the first broods of the two females, however, shows some differences: all the nestlings of the first-year female gained at the same rate and there was little variation between the weights of the individual birds; among the nestlings of the adult female, however, there was considerable variation. Also, the mean weights at the time of fledging of the nestlings of the first-year female were less than were those of the adult female's brood. The mean growth rates of the nestlings of the two broods were almost identical for the first ten days, but the rate of growth in the first-year female's brood decreased after ten days, while those of the adult female's brood continued

to be rapid for another two days. Weight variations during the rest of the nestling period were parallel in the two broods, but the mean weights of the nestlings of the first-year female remained 4 to 7 grams below those of the adult female's brood.

In the second brood, the development of the nestlings of the two females were similar throughout, until the death of the first-year female caused her brood to die on their thirteenth day. The rate of weight increase in the first nine days, if anything, tended to be more rapid in the first-year female's brood.

A comparison of the growth rates of the nestlings of the first-year female with the average weights of all nestlings (table 13) shows the same picture as the foregoing comparison. In the first brood, after the growth curves leveled off, the mean weights of the nestlings of the first-year female were well below the average weights; in fact, they were close to the minimum weights found in all first brood nestlings. In the second brood, however, the weight increases were more rapid in the brood of the first-year female than in the average nestling.

With brood weights available for only one first-year female, it is impossible to establish a significant difference between the growth of the broods of first-year and adult female starlings. Additional observations, however, further indicate the first-year females to be inefficient: During 1950 and 1951, five first-year females were known to have undertaken second broods, but none of these broods were fledged; some were deserted while still eggs, others after hatching (Kessel, 1953).

#### SEX RATIOS OF NESTLINGS

Little is known concerning the sex ratios of nestling birds. For the starling, Stresemann (1927-34) found a 50:50 sex ratio in nestlings at hatching. Bullough (1942b) reports 64, or 63.4 per cent, males of 101 young just off the nest, which is not statistically different from a 50:50 ratio ( $X^2=3.347$ ).

During the 1951 breeding season, all the nestlings on the Ithaca study area were collected so that sex ratios could be determined. The young were left in the nest until they were sixteen to eighteen days old; after this age nest mortality is negligible so figures thus obtained are essentially equivalent to sex ratios at the time the young leave the nest. Sex determinations are easily made through the examination of gonads; even ten-day incubated embryos can be sexed by gonad examination with a naked eye.

The results of the 1951 study are presented in table 15. The primary sex ratios (the proportion of sexes at the time of fertilization) were obtained by using the secondary sex ratios in nests where the entire clutch hatched and survived to the collection date. The secondary sex ratios (those at hatching) were obtained from nests in which all of the young that hatched survived to the collection date.

The 1951 data show a strong tendency toward a predominance of females among the Ithaca nestlings, the ratio being approximately 1.4 females to 1 male. Unfortunately, the sample numbers in most of the groupings in table 15 are too small to be significant. However, the primary sex ratio of 38.5 per cent males in the first brood, the secondary sex ratio of 39.4 per cent males for the entire season, and the sex ratio at the time of fledging of 43.5 per cent

TABLE 15.—Sex ratios of nestling starlings at Ithaca, New York, 1951

	Number Nests	Number ♂	Number ♀	Per cent ♂	Adjusted X <sup>2</sup>
Primary Sex Ratio					
First broods	18	35	56	38.5	4.396*
Intermediate broods	2	7	4	64.6	0.36
Second broods	4	6	9	40.0	0.27
Totals	24	48	69	41.0	3.418
Secondary Sex Ratio					
First broods	25	49	69	41.5	3.060
Intermediate broods	6	9	14	39.0	0.796
Second broods	7	11	13	45.9	0.044
Totals	38	69	96	39.4	4.048*
Sex Ratio at 16-18 days					
First broods	36	67	92	42.0	3.622
Intermediate broods	12	15	29	34.0	3.840
Second broods	17	31	26	54.4	0.280
Totals	65	113	147	43.5	4.188*

males for the entire season are significant. The few data available indicate that nest mortality is slightly higher in females than in males, the percent of males increasing during the period in the nest. This differential mortality is interesting in view of the results of most investigators who report a predominance of males in the adult population (see *Sex Composition*).

#### LEAVING THE NEST

Nestling starlings usually leave the nest on their twenty-first day after hatching. Some are capable of flight at nineteen days, and will leave the nest at that time if they are seriously disturbed. Others, however, for no obvious reason, stay in the nest beyond their twenty-first day. Not infrequently nestlings do not leave until their twenty-second day, and at least two broods on the Ithaca Study Area in 1950 did not leave until their twenty-third day. Bierman (1944) records a nest where the young did not leave until their twenty-fourth day, and Kluijver (1933) states that he has found a few in the nest as late as their twenty-fifth day.

Several days before leaving the nest, the young become extremely energetic, exercising both wings and legs. When being fed, they stick their heads far out the entrance hole to meet the incoming parents. Schüz (1943) records nestling starlings jumping out in front of their box to meet a parent coming with food as much as two days before finally leaving the nest.

When the young finally do leave the nest, they are almost as fully feathered as their adult parents. They are strong and, if necessary, can fly long distances as soon as they leave the nest. When they actually do fly from the box, however, they seldom go far. They may fly up into the tree in which their hole is located, or fly to a nearby tree, gable, or other convenient perch within 20 or 30 yards of the nest. The parents will usually follow the fledglings as they take their first flights from the nest, but if the

adult birds are not present at the time the nestlings leave, the young can be easily located by their loud call of "churr-churr."

All the young from a given nest do not always leave at the same time, some staying as long as two days after others have left.

After leaving the nest, the young are usually seen for at least a day in what appear to be family groups, usually with one parent tending several young. Within a few days family groups join together in flocks of ten to thirty juveniles, feeding independently with one or more adult birds usually among them.

At least some of these juveniles stay in the area of their place of hatching for a while after leaving the nest. This fact was evidenced at Ithaca on two occasions when a Cooper's hawk (*Accipiter cooperi*) fed to its nestlings banded, juvenile starlings that had been raised nearby and had been fledged for ten to twelve days. In the evenings the young starlings probably join communal roosts, as indicated by the one seen in such a roost on June 8, 1950, four days after leaving the nest; but some, at least, return to the vicinity of hatching to feed during the day.

Ball (1945) found that the early flocks near Grande Grève, Gaspé Peninsula, Quebec, did not go far. The young left the nest from July 8 to July 13, 1937, and by July 13 families were already banding together. From July 20 until August 26, a locally raised flock ranged the countryside over a distance of about one mile.

Kluijver (1935) states that some of the young leave the area of hatching soon after flying from the nest, but that others stay in the area until fall. Schüz and Weigold (1931) noted the same situation as Kluijver. Creutz (1939) states that, with some exceptions, the young leave the place of hatching soon after leaving the nest; they wander in all directions, but usually stay within 30 kilometers. He found that most of the birds moved to an area where feeding conditions seemed better.

In general, evidence indicates that the adults stay with the young for a relatively short time after they leave the nest. As soon as the young leave the nest, they are capable of doing some foraging for themselves. On June 4, 1950, the first day starlings left the nest at Ithaca, an adult was seen to feed a young starling several times, and between feedings the young seemed to forage for itself. A young starling was seen feeding by itself on June 8, 1950, after having been out of the nest a maximum of four days. It appeared to be completely independent, and no adult starling was seen in the vicinity during twenty minutes of observation. On this same day, a young starling, not four days fledged, was seen in a communal roost with cowbirds (*Molothrus ater*), grackles (*Quiscalus versicolor*), redwings (*Agelaius phoeniceus*), and other starlings.

Another indication that the parents do not stay long with the young after they leave the nest is that interest in second broods is manifested almost immediately after the young of the first broods leave. Elliott (1930) and Schüz (1943) noted the adults returning, unaccompanied, to the nesting site shortly after the young had left; Elliott found some returning as soon as the following day. He states (*op. cit.*: 74) that "oftentimes some of the old birds whose broods have departed return and will associate socially with others whose young have not as yet left the nest." At Ithaca, renesting

TABLE 16.—Nesting success of the starling, Ithaca, New York

	Eggs Hatched			Eggs Fledged			Young Fledged			Per cent Successful Nests	
	No. Eggs	No. Hatched	Per cent Hatched	No. Eggs	No. Fledged	Per cent Fledged	No. Young	No. Fledged	Per cent Fledged	No. Nests	1* 2†
1947	18	13	72.2	244	202	82.8	22	15	68.2	82	90.2
1948				59	46	78.0	67	63	94.0	60	71.7
1949	42	34	81.0	249	209	83.9	35	33	94.3	51	88.2
1950	249	228	91.6	209	157	75.1	194	157	80.9	52	73.1
1951	246	227	92.3	189	159	84.1	173	159	91.9	51	70.6
Total	555	502	90.5	950	773	81.4	491	427	87.0	296	79.7
1947				37	25	67.6				17	70.6
1948	20	16	80.0	20	12	60.0	36	28	77.8	22	68.2
1950	37	30	81.1							15	20.0
1951	62	53	85.5	58	41	70.7	47	41	87.2	19	68.4
Total	119	99	83.2	115	78	67.8	83	69	83.1	73	58.9
1947	43	30	69.8	96	61	63.5	32	20	62.5	44	63.6
1948	32	21	65.6	48	31	64.6	25	24	96.0	40	52.5
1950	106	89	84.0	52	39	75.0	45	39	86.7	41	34.1
1951	123	104	84.6	82	59	72.0	72	59	81.9	38	47.4
Total	304	244	80.3	278	190	68.3	174	142	81.6	163	49.7
Combined Totals (1947, 1948, 1950, 1951)	936	811	86.6	1094	832	76.1	713	605	85.2	532	67.7

\* Percent includes desertions caused by human disturbances

† Percent excludes desertions caused by human disturbances



activities become apparent immediately after the first brood has left in early June. Males come into full song; nest-building is renewed; and within six to ten days after the young have left two-thirds of the second brood layings have begun. In 1948 two females laid the first egg for the second brood a maximum of two days after the flying of the first brood, and one female only one day after the first brood left.

#### NESTING SUCCESS

Nesting success studies at Ithaca show the starling to be a relatively successful bird. The early nesting, or first broods, proved to be the most efficient nesting attempt of the season. An average of 90.5 per cent of the eggs hatched, and 87.0 per cent of the young fledged, giving an egg-to-fledging per cent of 81.4. (Unsuccessful nests are not included in fledging per cents.) The last, or second broods, yielded an average of 80.3 per cent of the eggs hatched, 81.6 per cent of the young fledged, and an over-all egg-to-fledging success of 68.3 per cent. The data obtained for the layings for intermediate broods are too few to be reliable, but they indicate a per cent of success intermediate between that of the first and second broods.

The per cent of successful nests, i.e., nests from which at least one bird was fledged, is also fairly high in the starling. In the first broods at Ithaca the nests averaged 89.1 per cent successful, but only 66.2 per cent successful for the intermediate broods and 63.3 per cent successful for the second broods.

The combined results of the nestings for the entire seasons of 1947, 1948, 1950, and 1951 show that 78.6 per cent of the nests were successful; 86.6 per cent of the eggs hatched, 85.2 per cent of the young fledged, and 76.1 per cent of the eggs that were laid produced young that were fledged. These total per cents tend to be weighted toward the averages of the early broods since more early nestings occur than later ones.

Table 16 gives more specific detail on the nesting success of the starling at Ithaca during the years 1947-51. The original field data varied somewhat in content from year to year, all data not being obtained from all the nests. The data in the table, therefore, are based on the material available under each individual heading, and the individual columns are not interrelated. The 1950 and 1951 nesting data are the most complete of the years tabulated.

The data on the per cent of successful nests are divided under two headings: Column 1 includes all nests, regardless of the cause of failure; column 2, excludes those failures caused by human disturbances. During the course of the Ithaca studies the nesting boxes were visited many times, and many of the adult birds, especially the females, were caught and banded. These disturbances caused a high per cent of desertions, and therefore significantly lowered the final per cent of successful nests. The low per cent of successful nests in the second brood in 1950 was due in large part to a high infestation of the blood-sucking larvae of *Protocalliphora*, one of the blow flies; and also, undoubtedly, to the extreme lateness of the 1950 season.

When compared with other starling nesting success studies, the Ithaca data appear somewhat different, though probably comparable. McAtee (1940) found that young were fledged from 86.9 per cent of 472 eggs over a four year period at Beltsville, Maryland. This per cent is high compared to the 76.1 per cent in 1094 eggs at Ithaca. Lack (1948a) reports that of 9,758

eggs tabulated from successful nests in Holland, 81 per cent hatched young that fledged. For some reason, Ithaca appears to have a lower egg-to-fledgling success than some other areas. The per cent of successful nests for the season compares closely with those of Kendeigh's (1942) in Ohio, the Ohio studies showing a 76 per cent success of nests for the season, and the Ithaca studies, 78.6 per cent. The nesting success of the starling appear to be higher than that of most birds, but tends to be comparable to that of other hole-nesters (cf. Allen and Nice, 1952; Kalmbach, 1939; Kendeigh, 1942; Nice, 1937).

#### COMPARISON OF FIRST AND SECOND BROODS

To summarize—second broods are fewer in number, and seem to occur less regularly than first broods. The clutches average fewer eggs, and the per cent hatch is lower than in first broods. The nestling mortality is higher, giving a lower per cent of nesting success and of successful nests. The young, too, when they leave the nest, are lighter in weight than those of the first brood, and their general physical condition appears poorer. In conclusion, the second broods are not as efficient as first broods, and in many years probably contribute little to the total population of starlings.

#### BREEDING OF FIRST-YEAR BIRDS

There has been much speculation as to whether or not starlings breed in their first year. Various studies have resulted in conflicting beliefs. In the final analysis, however, aided by the observations of banded birds, it can safely be stated that at least some starlings, both males and females, breed in their first year. Berndt (1939), Kluijver (1935), and Ticehurst (1913, 1914), as well as the present study, present banding data that prove the nesting of first-year birds.

Evidence does suggest, though, that more females than males nest in their first year. Bullough (1942b), in his studies on the reproductive cycles of the starling examined first-year females that shed eggs, but he never found a first-year male that even showed development of secondary spermatocytes. Vilks and von Transehe (1933) concluded from their observations that first-year males did not breed, but that the females did rarely. At Madison, Wisconsin, however, a first-year male was collected by the writer on April 5, 1949, and a cross-section of one of its testes revealed spermatozoa ready to free themselves from the Sertoli cells. This male would almost certainly have been capable of breeding that season. Evidence that some first-year males breed was obtained at Ithaca on May 12, 1950, when a banded male, hatched about May 6, 1949, was found sitting on three newly-hatched young and one unhatched egg. Further and more complete evidence on the breeding of first-year males is given by Kluijver (1935) for Dutch starlings. In his study he found four first-year males actually breeding, and thirteen first-year females. Since he found fifteen males apparently breeding for the first time at the end of their second or third year, and six females, he concluded that the greater part of the males breed at the end of the second year, and the greater part of the females at the end of their first.

The reason that so few of the first-year males nest can only be postulated. Some believe that the failure to breed is due primarily to immaturity, that

the first-year males are physiologically incapable of breeding. This hypothesis is undoubtedly true for some birds, since Savage (1922), Tischler (1908), and Witherby (1929) have collected first-year males from roosts during the breeding season with undeveloped testes. Not all non-breeding, first-year males, however, are immature. Again Tischler and Witherby have collected from communal roosts during the breeding season first-year males that had swollen testes, but apparently were not breeding.

Another factor often suggested to account for the infrequency of breeding among first-year males is the possible scarcity of females. Several studies have indicated that the sex ratio is unbalanced in favor of the males in the adult populations (see *Sex Composition*), and if the discrepancy is too great the young males, which apparently become sexually mature later in the season than the adult males, would be forced to remain unmated. The theory of the scarcity of females is not entirely tenable, however. In the course of the studies at Ithaca, New York, a large number of breeding females were removed from the Study Area after incubation and brooding had begun, but the males never seemed to have any difficulty in finding other mates. Throughout April and May the lost females were replaced within a day or two. Evidently there were extra, non-breeding females in the population.

One important factor in the non-breeding of first-year males appears to be the scarcity of holes for nesting sites. The availability of nesting sites seems to be the limiting factor in the size of the starling breeding population in most areas (Kessel, 1951b). Since the resident "old timers" on a given area are the first ones to preempt nesting sites for the coming season (see *Behavior During Winter*), and since adult birds (more than one year old) apparently become sexually mature before the first-year birds in the spring, few nesting sites are still available when the first-year males begin hunting for a place to nest.

Inheritance may also play an important part in the breeding of first-year birds. In 1949 the only two banded first-year females found breeding were sisters, banded together in a nest on June 9, 1948. In 1950, three of the six banded first-year birds found breeding were siblings (two females and one male), banded in the same nest on May 19, 1949; one of these females raised two broods in her first season.

No reliable estimate can be made from the data at hand as to the actual per cent of male or female starlings that breed in their first year. Such factors as mortality during the first year, and the per cent of those living that do not return to their place of hatching, are not known for the Ithaca area. Nevertheless, it is interesting to note that of eighty-nine females banded as nestlings in 1949 (a sex ratio of 43.5 per cent males, as found in the 1951 nestlings, assumed), five were actually found breeding during the 1950 season. Since roughly 60 per cent of the North American starlings die in their first year (see *Survival-Mortality*), a theoretical thirty-six of the banded first-year females were alive during the 1950 breeding season. Of these, five, or about 14 per cent, returned to their place of hatching and bred in their first year.

Birds breeding for the first time when about a year old tend to lay clutches somewhat smaller in size than do older birds (Lack, 1947-48). Kluijver (1935), from fifteen observations in Holland, found that the first-year females laid an average of only 4.7 eggs per clutch, while fifty-seven

adult females laid 5.9 eggs per clutch. In following first-year individuals through their first two seasons, he found that in eight instances out of eleven, clutches increased one or two eggs in the second year. At Ithaca, the average clutch for the first brood of twenty first-year females (most aged by hackles) from 1948 to 1951 (nineteen in 1950 and 1951) was 5.1 eggs. The average clutch of eighty-four adult females in 1950 and 1951 was 5.6 eggs. The difference between these two average clutch sizes is significant ( $t=2.371$ ).

Kluijver (1933, 1935) not only has evidence of smaller clutches, but he also shows that many first-year birds breed later in the season than the older birds; the date of the beginning of egg-laying for the first-year birds averages later than in older birds. There is considerable variation, however, in the times of egg-laying in first-year birds in relation to the times of adult layings. There are two to four consecutive days each year in which most of the starlings of a population begin egg-laying for the first brood, though a few will begin a few days earlier, and some a few days later. Of twenty-one first-year birds observed at Ithaca, ten laid during the heavy laying period when most of the rest of the population was laying; four laid a few days later; and seven laid in the group of layings for intermediate broods. No first-year birds at Ithaca are known to have laid in the earliest layings (the few days preceding the time of heaviest laying in the population).

Ithaca studies, then, show that some first-year birds may lay eggs later than some of the adult birds; and Kluijver shows that the average time of egg-laying for the first-year birds is later than adults. One can not conclude, however, as some have done, that the early, or first brood layings are those of adult birds, while those of the intermediate layings are first-year birds. On the contrary, at Ithaca and in Holland, the early layings include both adult and first-year birds; and at Ithaca, at least, most of the intermediate layings are apparently renesting attempts (see *Eggs*).

#### POST-JUVENAL AND POST-NUPTIAL MOLT

Within four to six weeks after the young leave the nest, many have begun their post-juvinal molt and are donning their first winter plumage. The post-juvinal molt is a complete molt, and the first-winter plumage closely resembles that of the adult birds; there are, however, some consistent differences (see Bullough, 1942a; Kessel, 1951a, and Witherby *et al.*, 1943). The feathers of the first-winter plumage are worn for a full year, the first nuptial plumage being acquired by the wearing off of many of the light feather tips. The full adult plumage is acquired in a complete post-nuptial molt during late June or early July of the second year. After the first post-nuptial molt, molts normally occur once each year—after the breeding season. This molt is complete; every feather on the body is changed, except when occasional abnormalities occur and some old feathers are retained. Plumage resulting from molts subsequent to the first post-nuptial molt are indistinguishable from the plumages of preceding years.

In the ensuing discussion on sequence of molt, the pterylography of the starling has been divided into eight feather tracts: alar, ventral, dorsal, humeral, femoral, crural, caudal, and capital (fig. 17). The molt pattern, based on the study of eighty-five fresh specimens collected near Ithaca, New York, appears to be the same for the juvenal, first-year, and adult plumages. The



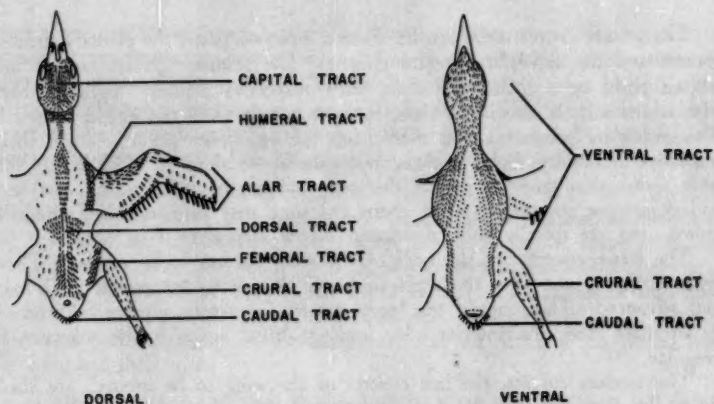


Fig. 17.—Pterylography of the starling. (Drawing by P. N. Adams.)

sequence is fairly regular within a given feather tract, but the tracts themselves proceed relatively independently of each other.

*Alar tract*—The first feather of the alar tract to be molted is the innermost primary, adult males shedding this feather during the last of June or the first week in July. The innermost primary is also the feather that usually initiates the complete annual post-nuptial or the post-juvenile molt. The molt of the primary feathers proceeds regularly from the innermost primary (primary I) outward to the outermost primary (primary X, or rudimentary primary). By August 1, some birds have advanced to the seventh primary stage (new primary VII developing); and by September 1, a few birds have reached the tenth primary stage, although some do not reach this stage until after September 15. At the time a given new primary is still sheathed, the primary preceding it is usually between one-third to two-thirds grown, and the one preceding this has almost completed its growth. Thus, the starling has only two non-functional primaries in a wing at a given time.

The molt of the secondary wing feathers commences with the shedding of the outermost secondary (secondary I), and progresses inward to the innermost, or secondary VI. The first secondary is molted during the middle of July, or about the time primary V is partially grown. Each new feather of this secondary series is somewhat further developed before the next is dropped than is the case with the primaries. The innermost secondary is usually the last feather of the entire alar tract to be molted, being retained even after primary X has been shed.

The tertials, sometimes considered a part of the secondary series, have a molt pattern of their own. The middle tertial drops first, about the time new secondary I begins growing. The innermost tertial is shed next, and both have reached full length before the last and outermost tertial has broken from its sheath. The entire tertial series is completely renewed before secondary III has reached full length.



The greater covert series can be divided into two parts, the primary greater coverts and the secondary greater coverts. The primary greater coverts are molted with, or a little later than, their respective primary flight feathers with which each is associated; thus, they, too, molt from the inside, outward. The secondary greater coverts molt from the outermost inward, as do their respective secondary flight feathers; but they are molted so rapidly that the molt seems simultaneous, several dropping out at the same time. The secondary greater coverts are shed about the time new primary II is one-half grown, and are usually fully developed before secondary I is molted.

The lesser coverts are the next of the wing coverts to be molted. They begin dropping out after the replacement of the secondary greater coverts is well advanced. The molt of the lesser coverts frequently appears to proceed by alternate rows, the anterior edge leading; often, however, the sequence is irregular.

The median coverts, the last coverts of the wing to be molted, are shed about the time primary VI is completing its growth and primary VII is one-half grown. The feathers of this series molt simultaneously and grow back rapidly.

The feathers of the carpo-metacarpal region are usually molted early, about the time the secondary greater coverts are molting.

Of the three large feathers of the alula, the proximal one is molted first. It is dropped at the same time, or shortly after, the feathers of the median covert series and at the time primary VI is completing its growth. It is completely replaced by the time the middle and distal feathers of the alula are molted. The middle and distal feathers are molted and renewed together.

The underwing coverts first show signs of molt at the anterior edge of the patagium, among the infra-marginal coverts. This area begins molting at the same time the lesser wing coverts on the upper surface of the patagium commence. The underwing carpal feathers are also molted at this time; the sequence is irregular, but the longer feathers are dropped before the shorter ones. The median series of the underwing coverts are the first of the major underwing coverts to be molted. The greater underwing coverts follow; and those near the infra-marginal coverts are last. The axillaries are molted with this latter series. The molt of these major underwing coverts proceeds from the proximal to the distal parts of the respective series. The underwing coverts are usually completely renewed by the time primary VIII is two-thirds grown.

The entire replacement of the feathers of the alar tract of the starling, from the time primary I initiates the molt until the replacement of either secondary VI or primary X closes it, requires a little over two months. Some birds shed the first feather of the alar molt during the last week in June; others are still in the final stages of the molt at the first of October.

*Ventral tract.*—The molt in the ventral tract begins early. Occasionally a few new pin-feathers appear even before primary I of the wing drops, but more frequently primary II completes its development before the first ventral tract feather is shed. The first signs of molt in the ventral tract appear in the anterior portion of the lateral branches of the tract. From here it first progresses posteriorly, though signs of its extension into the abdominal

region are not found much before the fourth primary stage. Somewhat later the molt progresses anteriorly where it meets the posterior development of the molt of the throat feathers. The molt of the ventral tract begins in the medial portions of the tract and proceeds laterally. The last feathers of the tract to be molted are the lateral ones in the abdominal region, which frequently persist to the last stages of the bird's entire molt.

*Dorsal tract.*—The dorsal tract often commences its molt simultaneously with the ventral tract. The molt usually begins in the widened, saddle-region of the back, but it sometimes starts more anteriorly in the scapular region. As with the ventral tract, the molt in the dorsal tract first proceeds posteriorly, and from the medial portions of the tract, laterally. Later, anterior extensions meet the molt from the crown and hind-neck. The regions at the base of the head and the region of the saddle are the last areas of the dorsal tract to complete their molt.

*Humeral tract.*—The molt in the humeral tract commences in the dorsal, anterior region of the tract shortly after the molt in the dorsal and ventral tracts has begun and proceeds forward to the junction with the ventral tract and backward over the scapular region.

*Femoral tract.*—The femoral tract frequently begins its molt shortly after the humeral tract but sometimes commences simultaneously with it. The molt proceeds from the anterior edge, posteriorly. Both the humeral and femoral tracts molt their feathers slowly, but they complete their feather replacements before the other contour feather tracts complete theirs.

*Crural tract.*—The crural tract is diffuse, except near the tarso-metatarsal joint, and its molt is irregular. The molt commences at about the same time as the other body tracts, and it is completed early. In general, it begins at the proximal end of the tibia and proceeds to the tarso-metatarsal region.

*Caudal tract.*—The first new feather of the caudal tract usually appears about the time primary III is completing its growth. Occasionally, however, the first rectrix will become evident even before primary II is fully grown. The most frequent sequence of molt in the caudal tract of the starling begins with the shedding of the two central tail feathers (pair I) and from there proceeds in a bilaterally symmetrical pattern. Pair II, adjacent to the central pair, drops out shortly after pair I. When pair II is about one-third grown, the outside, pair VI, is molted. After this, the tail molt may be irregular. Pair IV usually molts when pair VI is half-grown. Pair V and III follow, molting in rapid succession with V usually preceding III.

The molt of the upper and lower tail coverts is somewhat irregular. The time of molt is associated with that of the rectrices, but usually precedes them. The coverts nearest the base of the rectrices are shed first; then the series farther away. The coverts are completely replaced long before the rest of the molt of the caudal tract is completed. The completion of molt in the caudal tract coincides with the time primary VIII is two-thirds grown, the alula is being renewed, and the molt is beginning in the capital tract.

*Capital tract.*—The molt of the capital tract is a unique feature in the starling's molt pattern. Up until the time primary VI is fully grown there

is no sign of molt in the capital tract. At this late time birds in the post-juvenal molt are particularly striking. Superficially, the body, wings, and tail are dark with the new first-winter plumage, but the head and neck, not having begun to molt, are still completely mouse-brown in color.

The first signs of molt in the capital tract are on the medial line of the crown. From here the molt extends forward to the frontal region and backward to meet the advancing molt of the dorsal tract. Shortly after the first signs of new feathers appear in the crown region, new feathers appear almost simultaneously in the other series of the capital tract. A series, beginning in the gonydeal angle of the lower jaw and proceeding posteriorly, meets the rapidly advancing molt of the lower throat feathers of the ventral tract. The loreal region also shows early signs of molt which extend posteriorly and circle about the ocular region. A short series of supra-ocular feathers form a superciliary-like line over the eye. A series from the base of the upper mandible proceeds posteriorly and joins the original crown series, which widens and spreads over the crown and occipital region of the head. Finally, a series from the gape region extends posteriorly, circles, and includes the auricular region.

The molt of the capital tract usually begins by the third week in August, but the last feather of the capital tract to be replaced, one just dorsal to the auricular region, is sometimes retained until the middle of October.

There is considerable variation in the time of the molt of the starling, both in the relationships of the different tracts of an individual and between the members of the population. The most frequent sequence of molt in the tracts has been cited above. Deviations from this sequence are frequent, however, especially in young birds. For instance, while the innermost primary usually leads a new molt, it is not infrequent to find molt beginning earlier or simultaneously in the ventral or dorsal tract. And though the humeral and femoral tracts usually do not show signs of molt until after the dorsal and ventral tracts, a concurrent commencement is not infrequent.

Not all individuals of the population begin their molt at the same time. Generally, as a group, the adult males lead the molt, and, at any given time, will be the furthest advanced in their renewal of plumage. The adult females and juvenal males fall together, their molt beginning later than the adult males, but earlier than the juvenal females. The juvenal females lag behind the other groups (table 17).

Individuals within each of the groups may be retarded or advanced in

TABLE 17.—Development of the primary feathers as an indication of the stage of molt. Specimens collected from July 20 to July 23, 1947

Age and Sex	No. Specimens	Minimum Development Found	No. Found in Min. Stage	Maximum Development Found	No. Found in May Stage
Ad M	16	3rd primary $\frac{3}{4}$ dev.	2	6th primary $\frac{1}{4}$ dev.	2
Ad F	6	3rd primary $\frac{3}{4}$ dev.	1	4th primary $\frac{3}{4}$ dev.	4
Juv M	6	3rd primary $\frac{3}{4}$ dev.	2	4th primary $\frac{3}{4}$ dev.	4
Juv F	7	3rd primary $\frac{3}{4}$ dev.	5	5th primary $\frac{3}{4}$ dev.	1

their molt in relation to their group as a whole, and individuals of one group may approach the stage of molt of individuals of another group. For example, in specimens collected from July 20 to July 23, 1947, a juvenal female was taken whose molt had progressed farther than the molt of any of the adult females or juvenal males. At the same time, however, the juvenal females as a group still had a much higher per cent of the population at the minimum development than any other group (table 17).

Further indications of molt variations within specific groups are revealed in the adult male specimens. There are two specimens that have primary V still within the sheath, one from July 10 and the other from July 20; and two other specimens that have primary V almost fully developed, one on July 12, the other July 20. Of the adult females, a specimen from July 23, shows no indication of molt, whereas another from July 12, is already in the fifth primary stage.

#### POPULATION STATISTICS

##### SEX COMPOSITION

Studies on the adult sex ratios in starlings indicate that there is a preponderance of males in the population. Brouwer (1929) in Holland found proportions of 159 males to 146 females (1.1:1), and van Dobbin (see Kluijver, 1935) found 166 males to 124 females (1.3:1). Kluijver (1935), too, found a preponderance of males in Holland. Bullough (1942b), from 786 birds collected in England over a two year period, mostly in winter, found 71.1 per cent males (2.5:1).

In North America the male-female ratio for the starling appears similar to that found in northern Europe. Flicks (1934), in examining 2,522 birds, found an average of 67.9 per cent males (2.1:1) for the 1933-34 winter flocks at Columbus, Ohio. Odum and Pitelka (1939) collected 112 birds from an outdoor roost at Urbana, Illinois, on February 25-26 and found 68.7 per cent males (2.2:1); and on March 3-4, from 361 birds, found 64.3 per cent males (1.8:1). Loefer and Patten (1941) in collections made at Lexington, Kentucky, during the last week of March found only 45.3 per cent males from a total collection of 285 starlings (0.83:1). From a tower roost at Syracuse, New York, Stegman (1954) collected 455 starlings on March 28 and found that 52.7 per cent were males (1.1:1). At Ithaca, during winter bandings, an average of 58 per cent males was found (1.4:1) (table 18), but from the summer flocks a more balanced ratio was noted (table 19).

There are conditions that may alter a true 50:50 sex ratio and cause it to appear unbalanced, and it is a question how much of the difference found in the starling is real, and how much apparent. Since most of the data used for sex ratio studies have been gathered from massed flocks, and since the species shows few sexual dimorphisms, differences in brilliancy of plumage or display should have little effect on the results. Any differences in behavior between the sexes during various seasons of the year or during migration, however, could exert a profound effect. Results of banding operations at Ithaca during the spring of 1950, for instance, suggest the early migration of adult males. From March 15 to March 18, 107 starlings were trapped on the city dump: 54 adult males, 7 first-year males, 42 adult females, and 4 first-year females. On March 20 the first signs of starling migration were

TABLE 18.—Composition of winter flocks at Ithaca, New York

Date	Sex Ratios										All Birds	Locality
	Adult Males	First-year Males	Adult Females	First-year Females	Unaged Males	Unaged Females	Unsexed Birds	Total	Per cent Males in Total Sexed Population	Birds		
Dec. 7, '47	4	6	2	5	...	...	...	17	58.8	12:1	2:1	1.4:1 Vet. cupola
Dec. 20, '47	2	2	2	2	...	...	...	8	50.0	1:1	1:1	1:1 Vet. cupola
Jan. 13, '50	127	34	77	36	2	3	...	279	58.5	0.95:1	1.6:1	1.4:1 Lib. tower
Jan. 14, '51	44	8	48	21	...	...	...	121	43.0	0.38:1	0.92:1	0.75:1 Lib. tower
Feb. 5, '48	...	...	...	...	20	19	1	40	51.1	...	...	1:1 Dairy silo
Feb. 11, '48	...	...	...	...	40	21	...	61	65.6	...	...	1.9:1 Vet. cupola
Feb. 22, '51	37	5	19	5	1	...	...	67	65.6	1:1	1.9:1	1.8:1 Lib. tower
Feb. 22, '51	19	11	15	2	...	...	...	47	63.9	5.5:1	1.3:1	1.6:1 Dairy barns
Feb. 23, '47	...	...	...	...	8	6	...	14	57.0	...	...	1.3:1 Feeding sta.
Feb. 25, '50	178	57	142	51	3	8	...	439	54.3	1.1:1	1.3:1	1.2:1 Lib. tower
Feb. 26, '47	...	...	...	...	155	78	11	244	66.6	...	...	2:1 Vet. cupola
Mar. 15-18, '50	54	7	42	4	2	1	...	110	57.3	1.8:1	1.3:1	1.3:1 City dump
Total (incl. banded repeats)	465	130	347	126	231	136	12	1447	57.6	1:1	1.3:1	1.4:1
Total (excl. banded repeats)	432	127	314	124	226	136	12	1371	57.8	1:1	1.4:1	1.4:1



TABLE 19.—Composition of summer and autumnal flocks at Ithaca, New York

Date	Adult Males	First-year Males	Adult Females	First-year Females	Unaged Males	Unaged Females	Total	Locality
July 20, 1947	14	----	4	----	----	----	18	Vet. cupola (indoor)
July 23, 1947	2	6	2	6	----	----	24	Cattail roost
Aug. 25, 1948	2	4	1	5	----	----	12	Cattail roost
Oct. 9-10, 1950	12	15	15	18	----	----	60	Deciduous tree roost
Oct. 23, 1947	4	----	----	2	----	----	6	Alder thicket
Totals at outdoor roosts	20	25	18	31	----	----	102	

noted at Ithaca, and from March 23 to March 24, 122 starlings trapped were as follows: 73 adult males, 6 first-year males, 38 adult females, and 5 first-year females. While the proportion of first-year males and all the females remained about the same, the adult males increased. Van Dobbin (see Kluijver, 1935) found 60 per cent males from March 10-24, but only 48 per cent males from April 7-13. Loefer and Patten (1941) at Lexington, Kentucky, made their collections during the last week of March, the end of the migration period at that locality, and found only 45.3 per cent males.

Other differences in behavior between the sexes may affect sex ratios of collected birds in limited localities. At Ithaca, for instance, the per cent of males found in the winter roosts is relatively low until about the middle of February, at which time it increases and stays high (above 60 per cent) for about two weeks (table 18). A partial explanation for this variation may be the starling's habit of roosting at night in the breeding cavities. Some birds, especially the males, begin roosting at the nesting site as early as mid-December, and thus might lower the number of males using the communal roosts. After the middle of February, when larger numbers of females begin using the boxes (table 1), the relative per cent of males would rise again. How prevalent this shift toward the boxes is in the population is not known, but if it involves many birds, it could easily affect the sex ratios found at local communal roosts.

During the summer months the sex ratios in the field flocks and communal roosts may vary with several factors. In the actual breeding season the males sometimes resort to communal roosts at night, but at other times they may roost singly. After the young are seven to nine days old, the female, too, may or may not join the communal roosts for the night. After second broods have been started, the males may leave the nest site permanently and flock with other starlings. Some adult birds, instead of joining the large, mixed flocks after the completion of breeding activities, repair in small flocks to barns and cupolas.

In view of the different behavior patterns of the male and female starlings, it is difficult to determine the true sex ratio for the starling population as a whole. Most individual studies have included too few individuals for statistical significance, but the fact that so many studies have found more

males than females strongly suggests that there is actually an unbalanced sex ratio, favoring males, in adult populations.

If there is a preponderance of males in the adult starling population, a differential mortality rate between sexes is indicated. Sex ratios of nestling starlings at Ithaca show a predominance of females, but the per cent of males increases during the period in the nest (table 15). During the winter, six to eight months later, collections at Ithaca show an even sex ratio of first-year birds (table 18). And finally, as adults, the males appear to predominate: Of 812 adults caught during winters at Ithaca, 57.3 per cent were males ( $X^2=16.86^{**}$ ). The Ithaca data, then, indicate that the females have a higher mortality rate than the males.

#### LONGEVITY

The average expected longevity for the starling is about 1.5 years (see below); the turn-over period, the time required for a year class to shrink to an insignificant portion of the population, is about six years. A number of starlings, however, reach a much greater age. The maximum age recorded in the wild is apparently sixteen years (Loos, 1932; Jirsik, 1933). One bird of twelve years eight months has been recorded (Jirsik, 1934), as have a number of nine- and ten-year old birds (Anon, 1935; Flower, 1925; Junge, 1935; Kluijver, 1935; Schüz, 1933; and Witherby and Leach, 1934).

#### SURVIVAL AND MORTALITY

Several accounts on the age and survival of starlings have been published: Kluijver (1935) for birds in Holland, Lack (1943a, 1946b) in England, and Lack and Schifferli (1948) in Switzerland. The present compilations for North America are based on returns of birds banded in northeastern United States and Canada that were filed at the Bird-Banding Office of the U. S. Fish and Wildlife Service prior to June 30, 1954. The data are presented in the light of suggestions made in recent studies by Deevy (1947), Farmer (1945, 1949, 1952), Hickey (1952), Lack (1943a, 1943b, 1946b, 1948b), and Lack and Schifferli (1948); and they are subject to the same failings of hypothetical life table populations, sampling methods, and banding returns as are enumerated by these authors.

In order to study as uniform a population as possible, only banding returns from birds banded in the states or provinces of Michigan, Ohio, Indiana, Ontario, New York, Pennsylvania, New Jersey, Massachusetts, and Connecticut were used. The stability of this population might be questioned, but Davis (1950) presents data that indicate that the starling population, introduced in New York City in 1890, was stabilizing in northeastern United States around the 1930's. In view of the history of the western spread of the starling in North America and Davis' data, banding returns in the present study include only birds banded since 1928 in New York and Pennsylvania, since 1929 in Connecticut, Massachusetts, and New Jersey, since 1930 in Michigan, Ohio, and Indiana, and since 1933 in Ontario. No returns of bandings since 1946 are included from any area. Only returns indicating death have been used, but no attempt has been made to segregate deaths due to different causes—shooting, predation "found dead," etc. Unless otherwise indicated, all estimates of age and survival are calculated either from the first January 1 of life or the first January 1 after banding.

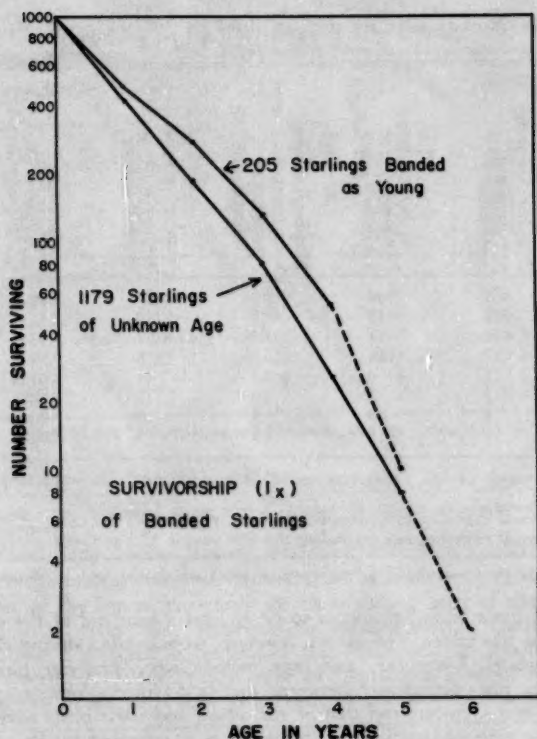


Fig. 18.—Survivorship of starlings banded in northeastern United States and Canada.

Only 205 returns are available for starlings that were banded as young and survived to their first January 1 of life. A life table based on these returns is presented in table 20. The mortality rate in the first year for this life table population is about 51 per cent. After the third year the mortality rates appear to increase with age (fig. 18). This apparent increase in mortality rates is not caused by distortions in calculated mortality rates (see Hickey, 1952), because the rates were calculated from actual deaths, nor is it likely to be caused by band losses (Hickey, 1952; Farner, 1952). The increased mortality may be actual, or it may result from the small size of the sample.

The mean annual mortality rate for this population of aged birds, calculated according to Farner (1945) and Lack (1948b), is about 50 per cent, whether the first year is included or excluded (table 20). The average length of life, after their first January 1, is 15.6 months, or 1.3 years.

Another life table, utilizing the deaths of 1179 starlings that were of unknown age at the time of banding is presented in table 21; the ages at death are calculated from the first January 1 after banding. Sixty-seven

TABLE 20—Life table for starlings, based on 205 young and beginning on their first January 1 of life

x	$l_x$	$d_x$	$l'_x$	$d'_x$	100qx	$e_x$
Age Interval in Years	Number Surviving at beginning of age interval	Number Dying in age interval	Number Surviving at beginning of age interval out of cohort of 1000	Number Dying in age interval out of cohort of 1000	Mortality Rate per year*	Expectation of Further Life (years)
0-1	205	104	1000	507	50.7	1.5
1-2	101	43	493	210	42.6	1.5
2-3	58	31	283	151	53.4	1.2
3-4	27	16	132	78	59.3	1.1
4-5	11	9	54	44	81.8	.9
5-6	2	1	10	5	50.0	1.5
6-7	1	0	5	0	00.0	1.5
7-8	1	1	5	5	100.0	.5

Average length of life (=expectation of further life on January 1) is 15.6 months, or 1.3 years.

Mean annual mortality rate, including the first year is 50.5 per cent.

Mean annual mortality rate, excluding the first year is 50.2 per cent.

\* Mortality rate calculated from actual number of deaths and survivors ( $l_x$  &  $d_x$ ).

per cent of these birds are known to be at least a year old at the commencement of the life table. The others, however, were banded during the months of July through December, and may include some first-year birds: Most banders do not distinguish between the first-winter plumage, gained in September and October, and that of the adult; and some birds were not aged at all at the time of banding. If, however, as is indicated by Farner (1945) and Lack (1946b), adult mortality rates in passerines are reached by the first January 1 of life, the inclusion of a few first-year birds in this life table will be inconsequential.

The annual mortality rate shown by this cohort of unaged birds is more constant than that shown in Table 20, the first three years showing a mortality rate of about 56 to 57 per cent (table 21, fig. 18). The increased mortality rate in the fourth and possibly the fifth years (= five + years actual age for most), while the cohort is still of moderate size, suggests an actual increase in mortality rate with age. Since the starling begins to breed in its first or second year, one would expect the starling to be in its "prime of life" from about 1 to 3 years. After that, an increased age-specific mortality rate might be expected. An increase is shown in the third and fourth years of the aged cohort (table 20), but the sample size is too small to be reliable.

The mean annual mortality rate for the unaged cohort, calculated according to Farner (1945) and Lack (1948b) is about 58 per cent. The average length of life after the first January 1 after banding is 12.4 months, or 1.0 years.

Monthly variations in the number of band recoveries each year show a striking pattern (table 22, Fig. 19). Each year a relatively large number of

TABLE 21.—Life table for starlings, based on 1179 birds of unknown age and beginning on the first January 1 after banding

x	$l_x$	$d_x$	$l'_x$	$d'_x$	100qx	$e_x$
Age Interval in years after Banding	Number Surviving at beginning of age interval	Number Dying in age interval	Number Surviving at beginning of age interval out of cohort of 1000	Number Dying in age interval out of cohort of 1000	Mortality Rate per year*	Expectation of Further Life (years)
0-1	1179	669	1000	567	56.7	1.2
1-2	510	286	433	243	56.1	1.2
2-3	224	127	190	108	56.7	1.1
3-4	97	66	82	56	68.0	1.0
4-5	31	22	26	18	71.0	.9
5-6	9	7	8	6	77.8	.9
6-7	2	2	2	2	100.0	.5

Average length of life (=expectation of further life on January 1) is 12.4 months, or 1.0 years.

Mean annual mortality rate is 57.5 per cent.

\* Mortality rate calculated from actual number of deaths and survivors ( $l_x$  &  $d_x$ ).

recoveries are made during January, February, and March, about 15 to 18 per cent of the annual recoveries occurring in each of these months. About 11 per cent of the annual recoveries are made during each of the months of April and May. After May, recoveries are reduced sharply, reaching a minimum of about 1 per cent in September, but rising only to about 6 per cent again in December. Undoubtedly some of this monthly variation is due to the availability of the recoveries as a result of climate and the habits of the

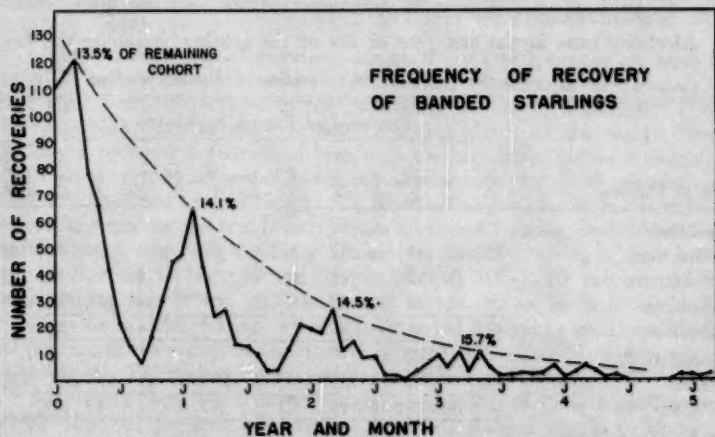


Fig. 19.—Monthly recoveries of 1179 unknown-age starlings banded in northeastern United States and Canada.



birds. Carcasses will not disintegrate as rapidly during the winter months as at other times of year, and wintering flocks of starlings usually gather near places of human habitation. On the other hand, during the early summer the birds are less gregarious and are engaged in breeding activities; and in the late summer and fall the flocks range widely over open fields and usually roost in marshes and thickets, thus making band recoveries less probable during these seasons than during the winter. It is not likely, however, that these extenuating circumstances account for all the monthly variations. In the region where these recoveries apply, the months of January, February, and March are the most severe of the year, both because of climatic conditions and the availability of food. From mid-February through March is also the period in which the migratory portions of the population of this region are moving to their breeding grounds. During April and May courtship and nesting activities are at their height, late nestings and second broods extending into June. October and November are the main months of the fall migration. It is improbable that the relationship of the number of recovered birds and the annual periods of environmental stress is pure chance. In lieu of more specific mortality data, for the purposes of the present calculations, the per cent of recoveries each month will be used as synonymous with the mortality occurring in those months.

When the monthly mortalities for each year of the unaged cohort's life span are examined separately (fig. 19), several interesting phenomena can be noted. First, each year, the mortality occurring in February-March is regularly about one-third (36, 38, 35, 26, 41 per cent, respectively) of the annual mortality; from January through May, the months of highest mortality, the rate is consistently three-fourths (74, 73, 73, 65, 75 per cent, respectively) of the annual mortality. (In the aged cohort, the per cents are about 30 and 70, respectively.) Second, the maximum monthly mortality occurring during the winter appears to be a constant per cent of the size of the cohort at that time, approximately 14 per cent (fig. 19).

Mortality rates in the first year of life of the starling, including the first

TABLE 22.—Monthly variation in recoveries of banded starlings

Age at Recovery	Frequency of Reports by Months												Size of Sample
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Aged Birds													
First Year	12	20	13	19	12	7	3	3	1	4	7	3	104
Adults	13	11	15	12	15	8	4	7	1	6	5	4	101
Total	25	31	28	31	27	15	7	10	2	10	12	7	205
Per cent	12.2	15.1	13.7	15.1	13.2	7.3	3.4	4.9	1.0	4.9	5.9	3.4	
Unaged Birds													
Total	191	212	210	124	121	74	46	27	17	25	51	81	1179
Per cent	16.2	18.0	17.8	10.5	10.3	6.3	3.9	2.3	1.4	2.1	4.3	6.9	
Aged & Unaged Birds													
Total	216	243	238	155	148	89	53	37	19	35	63	88	1384
Per cent	15.6	17.6	17.2	11.2	10.7	6.4	3.8	2.7	1.4	2.5	4.6	6.4	

summer, have been shown by Lack and Schifferli (1948) to be higher than in later years. Recoveries of birds banded in North America prior to June 1, however, are disappointingly few, causing the resultant mortality calculations to be tenuous. The first year mortality of a cohort of 37 juveniles banded before June 1 was 57 per cent. Forty-eight per cent of this first year mortality occurred from June through August. The average annual adult mortality (after the first year) of this cohort was 56 per cent.

The first year mortality of 81 birds banded before their first July 1 of life was 56 per cent, with an average adult mortality of 50 per cent per year. The first year mortality of 126 birds banded before their first August 1 was 60 per cent, with an average annual adult mortality of 40 per cent. Mortality rates derived through a comparison of productivity data with survivorship (page 324) show a 65 per cent mortality in the first year.

From the material available, then, mortality rates for the first year might be placed at approximately 60 per cent. Comparable adult mortality rates can be taken from the aged cohort in table 20 and placed at about 50 per cent. Corresponding rates for England and Switzerland given by Lack and Schifferli (1948) are 66 per cent first year, 52 per cent adult in England; and 73 per cent first year, 63 per cent adult in Switzerland.

A check can be made on the foregoing population studies by comparing productivity studies made at Ithaca with the survival-mortality studies based on banding returns. A productivity study in starlings, however, is complicated by the fact that many starlings do not breed in their first year. Few data are available to indicate the number of first-year birds that do breed, but indications are that they are few (see *Breeding of First-Year Birds*). For ease of calculations here, it is assumed that no starlings breed in their first year. This elimination of breeding in first-year birds is probably not serious in view of the fact that some adult birds apparently are non-breeders, "extras" always being available in the population to replace lost mates (Lack and Schifferli, 1948).

Using the mean annual mortality rate of 50 per cent from the life table in table 20 as a basis for productivity-mortality comparisons, on January 1 of a given year, 50 per cent of the population consists of adult birds (over one year old), and 50 per cent will be young (birds of the year). From January 1 to April 1 (month of breeding) the population suffers a mortality of 25 per cent (50 per cent of mean annual mortality rate of 50 per cent; see table 22, aged and unaged birds). Of the remaining birds, 89 per cent have successful nests for the first brood; broods average 4.5 young; and 87 per cent of the young are fledged. Since females successfully raising a first brood can be expected to begin second broods (Kessel, 1953), 89 per cent of the birds starting first broods will start second broods. These birds are successful in 63 per cent of their nests, have an average of 3.1 young each, and fledged 82 per cent of the young. (The number of intermediate broods, mostly renests, is unknown. To compensate in part for these nestings, the average brood size of 3.1 is used here which is the combined size for all "late brood" young (table 10); the per cent of successful nests and fledged young are those of second broods.) If the young are subjected to a mortality of 46 per cent between June 1 and January 1 they will make up 50 per cent of the total population on January 1. In the cohort of 37 juveniles banded before June 1,

32 per cent of the population died between June 1 and January 1. This cohort is too small for the figures to be reliable, however, and a mortality of 46 per cent is reasonable.

The mortality suffered by the adult and yearling members of the population is 50 per cent for the year. These productivity statistics, combined with the survival-mortality data, give the following results when applied to a population starting with 100 birds on January 1:

Start 100 birds (50 adult, potential breeders; 50 young, non-breeders).

Jan. 1 to Apr. 1 mortality of 25% leaves 37.5 adults to start breeding.

... 18.8 pairs start first broods

$18.8 \times 89\% = 16.7$  successful nests

$16.7 \times 4.5 = 75.2$  young

$75.2 \times 87\% = 65.4$  young fledged first brood

16.7 pairs start second broods

$16.7 \times 63\% = 10.5$  successful nests

$10.5 \times 3.1 = 32.6$  young

$32.6 \times 82\% = 26.7$  young fledged second brood.

Total in season = 92.1 young fledged

June 1 to Jan. 1 mortality of 46% of 92.1 young leaves 50 young alive on Jan. 1.

Jan. 1 to Jan. 1 mortality of 50% of 50 adults leaves 25 adults alive on Jan. 1.

Jan. 1 to Jan. 1 mortality of 50% of 50 yearlings leaves 25 yearlings (now adults) alive on Jan. 1.

... start new year on January 1 with same population as the preceding year—  
50 adults, 50 young.

By using the same mortality figures as above, two other calculations are possible. First, an alternate figure for mortality during the first year of life, beginning on June 1, can be derived by using the 46 per cent mortality from June 1 to January 1, and a 36 per cent mortality from January 1 to June 1 (72 per cent of mean annual mortality of 50 per cent occurs in the first five months of the year; see table 22, aged and unaged birds). These figures give a first year mortality rate of 65 per cent (see page 323).

A second calculation possible is that of the per cent of young that survive to breed. Assuming again that starlings do not breed until their second year, they suffer a 46 per cent mortality before their first January 1 of life, a 50 per cent mortality during their first year from January 1 to January 1, and a 25 per cent mortality between January 1 and April 1 in their second year before breeding. These mortality rates allow 20 per cent of the young fledged to survive to breed. This survival is similar to that found by other workers for various passerine species: 20 per cent for robins, *Turdus migratorius*, (Farner, 1945), 20 per cent for song sparrows, *Melospiza melodia*, (Nice, 1937), 17 per cent for starlings (Kluijver, 1935), 17 per cent for the house wren, *Troglodytes aëdon*, (Kendeigh, 1934), and 23 per cent in the European robin, *Erithacus rubecula* (Lack, 1943c).

#### SUMMARY

The preceding study on the breeding biology of the European starling (*Sturnus vulgaris* L.) was made at Ithaca, New York, from 1945 through 1951. The major portion of the study was carried out on an area of starling nesting boxes which bounded the periphery of a rectangular, agricultural district, 1.4 miles long by 0.8 mile wide.

Observations of the annual cycle show that many starlings of the resident population display an interest in nesting sites throughout the autumn and

winter months, both males and females visiting the holes in the mornings and evenings, especially in warm, sunny weather. By December some individuals begin roosting in the boxes at night, instead of returning to communal roosts; most of these early roosters appear to be ones that have previously nested on the area. Both males and females roost in the boxes. The number of birds using the boxes at night increases after mid-February, but decreases again when nest-building begins. Approximately 50 per cent of the birds nesting on the study area in one season return to breed the following year. These birds tend to choose nesting sites close to the ones they used the previous year.

The starling's nesting territory includes a 10- to 20-inch radius about the nesting hole. Starlings will nest in close proximity to other starlings and other species, although observations indicate that there is a limit to how close they will tolerate neighbors. They often have communal singing perches and feeding areas.

Courtship is not well defined in the starling, usually consisting of intensified song and display about the nesting box. Monogamy for a given nesting is the rule, though polygyny has been observed. The status of unpaired males is not well understood.

Both members of a pair participate in nest-building, which begins about the third week of March at Ithaca. The male frequently brings materials to the nest before he obtains a mate, but when serious nest-building begins, the female is usually the more diligent worker.

Copulation occurs upon the invitation of the female. The action of the female in pecking the male in the neck or shoulder region appears to be a "releaser" to the male in the mounting act.

The date of the laying of the first egg for the first brood varies from mid-March on the Gulf Coast to mid-June on the Labrador Peninsula. Day-length appears to be the primary factor influencing the date of egg-laying, but annual variations in egg-laying dates in a given locality appear to be due largely to temperature differences. The minimum threshold for incitement of rapid gonad development appears to be about 40 to 43°F, and the birds must be exposed to this mean environmental temperature for a minimum of seventeen days before they will lay eggs.

The mean clutch size in 301 layings at Ithaca was 4.9 eggs. In first broods the mean was 5.5 (199 clutches); in intermediate broods, 5.0 eggs (42 clutches); and in second broods, 4.1 eggs (110 clutches). Annual variations in mean clutch sizes proved significant. The mean weights of eighty-five eggs in sixteen first brood clutches was 7.0 grams (5.5-8.5 grams).

After the laying of the first egg, the female lays one egg a day until the clutch is completed. Females tend to lay clutches of similar size each year after the first year. Incubation usually begins with the laying of the last egg, though it may begin earlier. Incubation lasts for twelve days; it is usually shared by both parents, although only the female incubates at night. If a clutch is destroyed, at least one renesting will be attempted; most renestings begin within two weeks of the time the first nest is destroyed. If the female is lost during the incubation period, the male will toss the eggs out of the nest within thirty-six hours and renew his courtship activities.

The parents remove the shells of the hatched eggs by carrying them from the nest in their bills. Both parents brood and feed the young and participate

in nest sanitation. The female only, however, broods at night, staying with the nestlings in the box until they are eight days old. If the male disappears during the brooding period, the female usually continues to raise the family; however, if the female is lost the young usually die.

The mean brood size in 304 broods was 3.9 young. In first broods the mean was 4.5 young (230 broods); in intermediate broods, 3.5 young (41 broods); and in second broods, 2.9 young (78 broods). Comparisons with Dutch data on clutch and brood sizes and on egg-to-fledging success indicate that the starlings at Ithaca have a higher nest mortality than those on the Continent.

At hatching, the nestlings are helpless and naked, except for sparse tracts of down feathers, and weigh about 6.5 grams. Energy during the first ten to twelve days is utilized primarily for size increases. Weight gains, yielding a sigmoid growth curve, are rapid during this period, and at twelve days the weight of the young approaches that of the parent birds. Feathers do not begin to break their sheaths until the sixth and seventh days. Eyes open on the sixth or seventh day. At twelve days the nestlings begin to show signs of fear and attempt to escape when handled. After ten days, feather growth becomes rapid; and before the young leave the nest at twenty-one days, they are almost as fully feathered as their parents and can fly well. The young, especially in the first broods, usually lose some weight before they leave the nest.

In second broods the young are somewhat slower and more irregular in their development, usually averaging lighter than those of the first brood even at the time of fledging. There is some indication that the broods of first-year females may be poorer than those of adult birds. There is also some indication that mean nestling weights decrease as the size of the brood increases.

After leaving the nest, the birds gather in small flocks which rove about the countryside during the day and join communal roosts at night. Many juveniles apparently stay in the vicinity of their place of hatching for a while after leaving the nest. The young are largely independent when they leave the nest, and the adults stay with them for only a short time, about four to eight days.

Nesting success studies at Ithaca showed that 78.6 per cent of the nests were successful; 86.6 per cent hatched; 85.2 per cent of the young fledged; and 76.1 per cent of the eggs that were laid produced young that fledged. In first broods, these per cents were 89.1, 90.5, 86.0, and 81.4, respectively; in second broods they were 63.3, 80.3, 81.6, and 68.3 per cent, respectively.

Some starlings, especially females, breed when only one year old. In 1950, five, or 14 per cent of the banded female nestlings of the preceding year returned to their place of hatching and bred in their first year. The reason that more first-year males do not breed can be attributed, at least in part, to immaturity and to the lack of suitable nesting sites. The mean clutch size for the first brood of the first-year females was significantly smaller than that of the adults (5.1 and 5.6, respectively). Most first-year females begin laying for their first brood at the same time as the adult females, but some do not begin until the period of intermediate brood layings.

Within four to six weeks after the young leave the nest, many have



begun their post-juvenile molt. This molt is complete and follows the same pattern as that of the adult post-nuptial molt. The first-winter plumage is worn for a full year, until the first post-nuptial molt when the adult plumage is gained. After this second molt, the starling normally molts once each year, after the breeding season. The molt of the starling is essentially the same as that described by Dwight (1900) for passerine birds, but there are two major differences: 1) The capital tract does not begin to molt until the wing and body molts are well advanced. 2) The caudal tract, instead of molting consecutively from the central pair of feathers (pair I), outwards, usually molts pair I first, then pair II, pair VI, pair IV, and finally pair V and pair III. Generally, as a group, the adult males are the most advanced in their molt at any given time; the adult females and juvenile males follow; and the juvenile females are the least advanced.

There is a predominance of females in the sex ratios of nestling starlings, but nest mortality is slightly higher in the females, causing the per cent of males to increase during the period in the nest. During the winter, six to eight months later, collections show an even sex ratio in first-year birds. In adult populations there are significantly more males than females. Thus, data from Ithaca indicate that the females have a higher mortality rate than males.

On the basis of 205 banding returns of starlings that were banded as young and survived to their first January 1 of life, the mean annual adult mortality rate in the starlings of northeastern North America is about 50 per cent. The average length of life, after their first January 1, is 15.6 months. The months of heaviest mortality are January, February, and March. One-third of the annual mortality occurs in February-March; three-fourths from January through May. The mortality rate for the first year of life, including the first summer and autumn, is approximately 60 per cent. About 20 per cent of the young fledged survive to breed.

#### REFERENCES

- ALLARD, H. A. 1940—The starling's family life and behaviors. *J. Wash. Acad. Sci.* 30:34-46.
- ALLEN, R. W. AND M. M. NICE 1952—A study of the breeding biology of the purple martin (*Progne subis*). *Amer. Midl. Nat.* 47:606-665.
- ANDREWS, W. J. 1915—Unusual nesting-sites. *Brit. Birds* 9:180.
- ANONYMOUS 1935—Recovery of marked birds. *Ibid.* 29:51.
- ARMSTRONG, E. A. 1947—Bird display and behaviour. Revised Ed. (Oxford Univ. Press, N. Y.).
- BAKER, J. R. 1938—The relation between latitude and breeding seasons in birds. *Proc. Zool. Soc. (London)* A108:557-582.
- BALL, S. C. 1945—European starling in Gaspé. *Auk* 62:79-97.
- BARTH, E. K. 1953—Calculation of egg volume based on loss of weight during incubation. *Ibid.* 70:151-159.
- BAYNE, C. S. 1933—The sexual chase among starlings. *Brit. Birds* 27:104-106.
- BENT, A. C. 1950—Life histories of North American wagtails, shrikes, vireos, and their allies. *U. S. Nat. Mus. Bull.* 197.
- BERNDT, R. 1939—Untersuchungen über die zweite Brut beim Star (*Sturnus v. vulgaris* L.) im Braunschweiger Hügelland. *Vogelzug* 10:7-16.

- BETHAM, R. M. 1929—Some observations on the nesting of birds in the vicinity of Cape Town, South Africa. *Ibis* 5(series 12):71-105.
- BEVEN, G. 1946—Courtship presentation by starling. *Brit. Birds* 39:116.
- BIDWELL, E. 1896—List of Western Palaearctic birds in the nest of which cuckoos' eggs have been found. *Bull. Brit. Ornithologists' Club* No. 34. (Printed in *Ibis*, 2(series 7):397-400)
- BIERMAN, D. R. 1944—A starling nesting study. *Passenger Pigeon* 6:46-48.
- BISSENETTE, T. H. 1930—Studies on the sexual cycle in birds. I. Sexual maturity, its modification and possible control in the European starling (*Sturnus vulgaris*): a general statement. *Amer. J. Anat.* 45:289-305.
- AND M. H. CHAPNICK 1930—Studies on the sexual cycle in birds. II. The normal progressive changes in the testis from November to May in the European starling (*Sturnus vulgaris*), an introduced, non-migratory bird. *Ibid.* 45:307-343.
- AND A. P. R. WADLUND 1931—Studies on the sexual cycle in birds. VII. Spermatogenesis in *Sturnus vulgaris*. Refractory period and acceleration in relation to wave length and rate of increase of light ration. *J. Morph.* 52:403-427.
- AND A. J. ZUJKO 1936—Normal progressive changes in the ovary of the starling (*Sturnus vulgaris*) from December to April. *Auk* 53:31-50.
- BLAGG, E. W. H. 1893—Notes on the nesting of some Shetland birds. *Ibis* 5(series 6): 350-358.
- BLOCHER, A. 1933—Losses. *Oölogist* 50:157.
- BODENSTEN, A. 1935—Starling and flicker nesting together. *Ibid.* 52:132.
- BROUWER, G. A. 1929—Overzicht van de vogels aangevlogen tegen den vuurtoren 'Het Westhoofd' op Goeree gedurende de jaren 1924 t/m 1928. *Ardea* 18:140-161.
- BULLOUGH, W. S. 1942a—On the external morphology of the British and Continental races of starling (*Sturnus vulgaris* Linnaeus). *Ibis* 6:225-239.
- 1942b—The reproductive cycles of the British and Continental races of the starling (*Sturnus vulgaris* L.). *Philos. Trans. Roy. Soc. (London)*, B 231: 165-246.
- BURGER, J. W. 1939—Some aspects of the roles of light intensity and the daily length of exposure to light in the sexual photoperiodic activation of the male starling. *J. Exp. Zool.* 81:333-341.
- 1940—Further studies on the relation of the daily exposure to light to the sexual activation of the male starling (*Sturnus vulgaris*). *Ibid.* 84:351-361.
- 1948—The relation of external temperature to spermatogenesis in the male starling. *Ibid.* 109:259-266.
- 1949—A review of experimental investigations on seasonal reproduction in birds. *Wilson Bull.* 61:211-230.
- 1953—The effect of photic and psychic stimuli on the reproductive cycle of the male starling, *Sturnus vulgaris*. *J. Exp. Zool.* 124:227-239.
- BURLEIGH, T. 1944—The bird life of the Gulf Coast region of Mississippi. *Occ. Papers Mus. Zool. La. Univ.*, No. 20:329-490.
- CHAPMAN, F. M. —1925—The European starling as an American citizen. *Nat. Hist. (N. Y.)* 25:480-485.
- CHAPPELL, B. M. A. 1949—Courtship feeding of starling. *Brit. Birds* 42:118-119.
- COOK, MRS. H. P. 1934—Some scattering bird notes from Indiana. *Wilson Bull.* 46: 202-203.
- CREUTZ, G. 1939—Biologische Beringungsergebnisse bei Staren, *Sturnus v. vulgaris* L. *Mitt. Ver. Sächs. Ornith.* 6:18-26.
- DAVIS, D. E. 1950—The growth of starling, *Sturnus vulgaris*, populations. *Auk* 67: 460-465.
- DEEVEY, E. S. 1947—Life tables for natural populations of animals. *Quart. Rev. Biol.* 22:283-314.
- DOOLITTLE, E. A. 1926—A community nesting tree. *Wilson Bull.* 38:115.

- DIGHT, J. 1900—The sequence of plumages and moults of the passerine birds of New York. *Ann. N. Y. Acad. Sci.* 13:73-360.
- ECKARDT, W. R. 1919—Aussereheliche Bruten bei monogamen Vögeln. *Ornith. Monatsberichte* 27:84-85.
- ELLIOTT, J. S. 1930—The nesting period of the starling. *Brit. Birds* 24:73-74.
- ENGLISH, T. M. S. 1917—Starling nesting in a laurel bush. *Brit. Birds* 11:44.
- FARNER, D. S. 1945—Age groups and longevity in the American robin. *Wilson Bull.* 57:56-74.
- 1949—Age groups and longevity in the American robin: comments, further discussion, and certain revisions. *Ibid.* 61:68-81.
- 1952—The use of banding data in the study of certain aspects of the dynamics and structure of avian populations. *Northwest Science* 26:41-50, 79-94, 119-144.
- FLOWER, S. S. 1925—Contributions to our knowledge of the duration of life in vertebrate animals. IV. Birds. *Proc. Zool. Soc. (London)* 1925:1365.
- FREITAG, F. 1936—Aus dem Leben beringter Stare zur Fortpflanzungszeit. *Vogelring* 8:8-15.
- 1937—Aus dem Leben beringter Star zur Fortpflanzungszeit II. *Ibid.* 9:43-49.
- 1939—Aus dem Leben beringter Stare zur Fortpflanzungszeit. *Ibid.* 11:1-9.
- 1940—Beobachtungen an beringten Staren zur Brutzeit. *Ibid.* 12:13-15.
- FRIEDMANN, H. 1934—Further additions to the list of birds victimized by the cowbird. *Wilson Bull.* 46:25-36; 104-114.
- GIBB, J. 1950—The breeding biology of the great and blue titmice. *Ibis* 92:507-539.
- GLADSTONE, H. S. 1910—Birds of Dumfriesshire, A Contribution to the fauna of the Solway area. (Witherby & Co., London).
- GODFREY, R. 1935—The islands of Yell and Sound Bigga. *Blythwood Review (Cape Colony)*, Oct. :119-120.
- GODMAN, F. D. 1866—Notes on the birds of the Azores. *Ibis* 2(series 2):88-109.
- GRABHAM, O. 1895—Polygamy in the starling. *Zoologist*, 19(series 3):307-308.
- GREER, T. R. 1929—*Oölogist* 46:88.
- HEWETT, W. 1881—Starling and stock dove laying in the same nest. *Zoologist* 5(series 3):65.
- HICKEY, J. J. 1952—Survival studies of banded birds. Special Scientific Report: Wildlife No. 15. Fish and Wildlife Service, U. S. D. I.
- HICKS, L. E. 1934—Individual and sexual variations in the European starling. *Bird-Banding* 5:103-118.
- HOYT, J. S. Y. 1948—Observations on nesting associates. *Auk* 65:188-196.
- JIRSIK, J. 1933—Der Zug des auf dem Gebiet der tschechoslovakischen Republik nistenden Stares *Sturnus v. vulgaris* L. German translation of paper submitted in May 1933 to the Masarykova Akademie, Prague. (Reviewed in *Bird-Banding* 5:142).
- 1934—An interesting result of our ringing and some foreign ringed birds caught in Czechoslovakia. *Sborník zoolog. odd. Nar. Musea v Praze* I 18:52-53. (Reviewed in *Bird-Banding* 6:109).
- JUNGE G. C. A. 1935—Resultaten van het ringonderzoek den vogeltrek, ingesteld door het Rijkmuseum van Natuurlijke Historie te Leiden. *Ardea* 24:116-199.
- KALMBACH, E. R. 1939—Nesting success: Its significance in waterfowl reproduction. *Trans. 4th N. A. Wildlife Conference* :591-604.
- KENDEIGH, S. C. 1934—The role of environment in the life of birds. *Ecol. Monogr.* 4:299-417.
- 1942—Analysis of losses in the nesting of birds. *J. Wildlife Mgt.* 6:19-26.
- KESSEL, B. 1950—Observations on the polygamy and territorial behavior of a male starling (*Sturnus vulgaris*). *Bird-Banding* 21:112-114.

- 1951a—Criteria for sexing and aging European starlings (*Sturnus vulgaris*). *Ibid.* 22:16-23.
- 1951b—Investigations on the life history and management of the European starling (*Sturnus vulgaris vulgaris* L.) in North America. Thesis for degree of Ph.D., Cornell University. (Unpublished).
- 1953—Second broods in the European starling in North America. *Auk* 70:479-483.
- KLUIJVER, I. H. N. 1933—Bijdrage tot de biologie en de ecologie van den spreeuw (*Sturnus vulgaris vulgaris* L.) gedurende zijn voortplantingstijd. Versl. Meded. Plantenziekt. (Wageningen) 69:1-145.
- 1935—Waarnemingen over de levenswijze van den spreeuw (*Sturnus vulgaris*) met behulp van geringde individuen. *Ardea* 24:133-166.
- KOHLER, L. S. 1915—An unusual nesting colony. *Oölogist* 32:81.
- LACK, D. 1943a—The age of some more British birds. *Brit. Birds* 36:193-195, 214-221.
- 1943b—The age of the blackbird. *Ibid.* 36:166-175.
- 1943c—The life of the robin. (H. F. & G. Witherby, Ltd.).
- 1946a—Clutch and brood size in the robin. *Brit. Birds* 39:98-109, 130-135.
- 1946b—Do juvenile birds survive less well than adults? *Ibid.* 39:258-264.
- 1947-48—The significance of clutch-size, Parts I, II & III. *Ibis* 89:302-352; 90:25-45.
- 1948a—Natural selection and family size in the starling. *Evolution* 2:95-110.
- 1948b—Notes on the ecology of the robin. *Ibis* 90:252-279.
- 1949—Family size in certain thrushes (*Turdidae*). *Evolution* 3:57-66.
- AND A. SCHIFFERLI 1948—Die Lebensdauer des Stares. *Ornith. Beobachter* 45:107-114.
- AND E. T. SILVA 1949—The weight of nestling robins. *Ibis* 91:64-78.
- LEES, J. 1949—Weights of Robins—Part 1. Nestlings. *Ibid.* 91:79-88.
- LEWIS, H. F. 1935—Nesting of the starling (*Sturnus vulgaris vulgaris*) in the Labrador Peninsula. *Auk* 52:313.
- LEWIS, S. 1899—Starlings nesting in fir trees. *Zoologist* 3(series 4):370.
- LOEFER, J. B. AND J. A. PATTEN 1941—Starlings at a blackbird roost. *Auk* 58:584-586.
- LOOS, K. 1932—Bericht über die Tätigkeit der ornithologischen Station 'Lotos' in Liboch a. d. Elbe für das Jahr 1931. *Lotos* 80:65.
- LOVELL, H. B. AND W. M. CLAY 1942—Nesting of the starling in Kentucky. *Kentucky Warbler* 18:29-34.
- MCATEE, W. L. 1940—An experiment in songbird management. *Auk* 57:333-348.
- MARPLES, G. 1936a—Behaviour of starlings at nesting site. *Brit. Birds* 30:14-21.
- 1936b—Further notes on behaviour of starlings at the nesting site. *Ibid.* 30:41-42.
- MARSHALL, A. J. 1951—The refractory period of testis rhythm in birds and its possible bearing on breeding and migration. *Wilson Bull.* 63:238-261.
- MAY, D. J. 1947—Courtship display of starling. *Brit. Birds* 40:48.
- MORLEY, A. 1941—The behaviour of a group of resident British starlings (*Sturnus v. vulgaris* Linn.) from October to March. *Naturalist* 1941:55-61.
- MUSSELMAN, T. E. 1942—A probable case of parasitism of the starling. *Auk* 59:589-590.
- NETHERSOLE-THOMPSON, D. AND D. W. MUSSELWHITE 1940—Display of starlings. *Brit. Bird* 34:44.
- NEWSTEAD, R. 1908—The food of some British birds. *J. Board Agr. Suppl.* No. 9.
- NICE, M. M. 1937—Studies in the life history of the song sparrow. Vol. I. *Trans. Linnaean Soc. of N. Y.* 4:1-247.
- ODUM, E. P. AND F. A. PITELKA 1939—Storm mortality in a winter starling roost. *Auk* 56:451-455.

- PORTMANN, A. 1938—Beiträge zur Kenntnis der postembryonalen Entwicklung der Vögel. I. Vergleichende Untersuchungen über die Ontogenese der Hühner und Sperlingvögel. *Rev. Suisse Zool. (Genève)* 45:273-348.
- ROBINSON, H. W. 1930—Starling nesting in fork of tree. *Brit. Birds* 23:253.
- SAVAGE, E. U. 1922—Some observations on the flocking of starlings. *Brit. Birds* 16: 77-78.
- 1929—Starling (*Sturnus v. vulgaris*) nesting in fork of tree. *Brit. Birds* 23:189.
- SCHANTZ, W. E. 1938—The three bachelors. Unpublished manuscript.
- SCHÜZ, E. 1933—Ring-Wiederfunde auswärtige Stationen 8. *Vogelzug* 4:168-171.
- 1942—Biologische Beobachtungen an Staren in Rossitten. *Ibid.* 13:99-132.
- 1943—Brutbiologische Beobachtungen an Staren 1943 in der Vogelwarte Rossitten. *J. Ornith.* 91:388-405.
- AND H. WEIGOLD 1931—Atlas des Vogelzugs nach den Beringungsergebnissen bei palaearktischen Vögeln. . . . (Kommissions-Verlag: R. Friedlander und Sohn, Berlin).
- SOPP, A. 1932—Kleinere Beobachtungen aus dem Jahre 1931. *Mitt. Vogelw.* 31:27.
- STEGEMAN, L. C. 1954—Variation in a flock of the European Starling. *Auk* 71:179-185.
- STONER, D. 1942—European starling nesting in a bank swallow burrow. *Wilson Bull.* 54:215.
- STRESSEMAN, E. 1927-34—Handbuch der Zoologie 7(2), Aves. (Berlin and Leipzig).
- TICEHURST, N. F. 1909—Starlings nesting sites. *Brit. Birds* 3:118-120.
- 1913—Recovery of marked birds. *Ibid.* 7:9.
- 1914—Recovery of marked birds. *Ibid.* 8:45.
- TISCHLER, F. 1908—Star-Ansammlungen zur Brutzeit. *Ornith. Monatsberichte* 16:21-26.
- VILKS, K. AND N. VON TRANSEHE 1933—Ergebnisse der Beringung von Staren in Lettland. *Vogelzug* 4:113-118.
- WALLRAFF, H. G. 1953—Beobachtungen zur Brutbiologie des Stares (*Sturnus v. vulgaris* L.) in Nürnberg. *J. Ornith.* 94:36-67.
- WARGA, K. 1938—Tägliche Gewicht-Zunahme während der Fütterungs-Zeit bei *Parus m. major*, *Phoenicurus p. phoenicurus*, *Sylvia atricapilla*, *Serinus canarius serinus* und *Sturnus v. vulgaris*. 9me Congr. Orn. Int., Rouen: 523-534.
- WEBER, J. A. 1907—Abstr. *Proc. Linn. Soc. N. Y.* Nos. 17-19:15.
- WITHERBY, H. F. 1929—Breeding starlings resorting to a roost. *Brit. Birds* 23:187-189.
- AND E. P. LEACH 1934—Movements of ringed birds from abroad to the British Isles and from the British Isles abroad. *Addenda III. Ibid.* 28:106-112.
- , REV. F. C. R. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER 1943—The Handbook of British Birds, Rev. Ed., Vol. I. (H. F. & G. Witherby Ltd., London).



## Some Aspects of the Hematology of Turtles as Related to Their Activity<sup>1</sup>

Albert E. H. Gaumer<sup>2</sup> and Clarence J. Goodnight  
Purdue University, West Lafayette, Indiana

The physiological characteristics of animals are correlated with the animal's activity as well as with their evolutionary history. Since blood is one of the best tissues for studying this correlation, an investigation was made on certain aspects of the blood chemistry of turtles. This investigation included the measuring and counting of the erythrocytes, the determination of the hemoglobin content and pH, the calculation of the specific gravity of the blood, and the accumulation of data for the oxygen and carbon dioxide dissociation curves.

Turtles were chosen as experimental animals for the following reasons: their morphology and taxonomy have been adequately explored; differentiation between sexes is relatively simple; their habitats vary from terrestrial to aquatic; they are readily available; and finally they are easily kept under laboratory conditions.

A number of important studies have contributed information to our knowledge of turtle hematology. These include investigations by Southworth and Redfield (1926), Redfield (1933), Tipton (1933), and Wintrobe (1933). Of these, the one most pertinent to the present study was that by Southworth and Redfield (1926) concerning the oxygen dissociation curve of *Pseudemys concinna*. Much of the data from the above cited papers and various other sources is summarized by Albritton (1952).

While these various studies have contributed much to the understanding of turtle hematology, little has been done toward comparing the physiological characteristics of various species as a possible basis for understanding their activities. It is the purpose of the present study to compare the hematology of four different species and if possible to correlate the data so obtained with the activity of the turtles.

### MATERIALS AND METHODS

Four species representing four different genera of turtles were used in the investigations in this study. They were as follows: *Terrapene c. carolina* (Linné), *Pseudemys scripta troostii* (Holbrook), *Chrysemys picta marginata* Agassiz, and *Chelydra s. serpentina* (Linné). These animals were obtained from Steinhilber Supply Company, Hoffman Supply, Incorporated, and the Carolina Biological Supply House and were maintained in tanks. These tanks, which were constructed of concrete and lined with a coat of paraffin, were 130 cm by 72 cm. For the aquatic species, the water, which was constantly flowing into and out of the tanks, was unchlorinated and was maintained at a depth of approximately 25 cm. Platforms of wood were provided for the animals to crawl up onto out of the water. In the case of the terrestrial species, the surface of the tank was kept dry with water available only in sufficient quantities for drinking. Once a week the turtles were fed horsemeat and lettuce. No force feeding was necessary since these

<sup>1</sup> Research supported in part by a fellowship from the Purdue Research Foundation.

<sup>2</sup> Present address: Department of Biology, Moravian College, Bethlehem, Pennsylvania.

animals ate well in captivity. For purposes of identification, these turtles were marked according to the system of Cagle (1939).

The blood was withdrawn from the turtle by the following method. A brace with a 1/16 inch bit was used to drill into the plastron, making an opening in the median anterior corner of the right abdominal plate. This drilling operation was done with extreme care so as to penetrate only the plastron and not to touch the underlying organs. After the opening was made into the plastron, a number 19 hypodermic needle was inserted into the heart. In order to penetrate the rather leathery pericardium, the needle had to be inserted with a "thrust" motion. Autopsies revealed that the ventricle of the heart was punctured by this method. This was also evident from the coloration and pulsation of the blood flow in the syringe.

After the drawing of the blood was completed, the turtle was literally "corked" shut. A number 000 cork was inserted into the opening in the plastron and was then trimmed flush with the plastron surface. The turtle was returned to its original tank until it was again needed. A minimum of three days elapsed between each bleeding.

For most tests, blood was transferred under oil to a vial coated with heparin. In the blood used for the cell pack volume (hematocrit value), a mixture of potassium and ammonium oxalate was used as the anti-coagulant since this does not interfere with sedimentation while heparin does. The blood was then transferred to hematocrit tubes of the Wintrobe type. These tubes were then centrifuged for thirty minutes at 3000 revolutions per minute according to the method of Wintrobe as outlined by Hepler (1950).

The equilibration of the blood was carried out in the following manner. The blood was equilibrated at known tensions of carbon dioxide and oxygen in a tonometer placed in a constant temperature bath for a given period of time. The temperature chosen was 25° C because that is the approximate temperature of the body of the turtle. The blood was then analyzed in a Van Slyke manometric apparatus. The tonometer in which the blood was equilibrated was prepared in advance of the drawing of the blood. These tonometers were of the Barcroft type. The general formula for computing the amount of gas to be added is as follows:

$$\text{ml gas to be added to the tonometer} = \frac{(\text{pressure of the gas}) \times (\text{volume of tonometer})}{(\text{barometric pressure})}$$

Five milliliters of the blood were introduced into the tonometer through the stopcock. With another syringe, mercury was forced through the stopcock until the capillaries of the bores were completely filled. The time was noted and the tonometer was placed in the constant temperature bath set at 25° C where it was rotated by means of a mechanical rotator. Thirty minutes equilibration was used to insure complete equilibrium of the blood with the gases. The blood gases were then determined using the modified manometric procedure from Van Slyke and Neill (1924). The percentages of gases in the tonometers were determined by use of the Haldane gas analysis apparatus and the partial pressure estimated using the modified formula of Bock, Field, and Adair (1924).

The enumeration of the erythrocytes was done by standard techniques. In order to insure a more nearly reliable result, five individual counts were

made from each pipette and then the average was taken as the final count. Measurements of red blood cells sizes were made by means of a Spencer micrometer using blood smears which were stained with Wright's stain. The width and length of 500 cells were measured and representative measurements of blood samples were taken from 12 individuals of each species. Counts were made on the standard hemocytometer with the improved Neubauer Ruling.

Counts of the leucocytes were not possible because solutions which would luke the erythrocytes would also destroy the leucocytes.

The specific gravity of the whole blood was obtained by the dropping copper sulphate method of Phillips *et al.* (1950).

The Dare hemoglobinometer was used in the determination of the hemoglobin content. This was checked by the method of Evelyn and Malloy (1938) using the Klett photometer.

A Beckman glass electrode pH meter was used in determining the pH of the blood.

#### OBSERVATIONS AND RESULTS

The sizes of the erythrocytes are given in table 1. It is of interest to note that the cells of *Chelydra* were the longest and the widest of the cells examined. The product of the length (L) and the width (W) gives some indication of the size of the cell. In reference to these data, *Chelydra* is shown to have the largest cells. The quotient of the length (L) divided by the width (W) presents a comparison of the cell shape. A comparison of these results shows that the blood cell shape of all the species examined was essentially the same.

Interesting results were obtained in relation to the red blood cell count. Again *Chelydra* blood proved to be markedly different from the bloods of the other three species in that its cell number was significantly lower than the numbers of the other bloods. In hemoglobin content, on the other hand, blood of *Chelydra* had the greatest amount of hemoglobin. It may be noted that there is a gradual increase in the hemoglobin content of the bloods advancing from the blood of the terrestrial species to the blood of the aquatic species.

The specific gravities showed no marked differences. Similarly, the pH of all the bloods was practically the same for all species concerned (table 2).

Interesting data were found in the comparison of the oxygen dissociation curves. Table 3 shows how the blood of *Terrapene* is similar to fetal blood of mammals in its ability to carry oxygen. Of especial interest is the point (40 mm Hg pressure) at which all of the bloods examined exhibit a saturation of approximately 82% oxygen.

In the case of *Chrysemys*, which may be considered to be somewhat

TABLE 1.—Comparison of red blood cell sizes in turtles. All measurements in micra.

Species	Length	Width	L X W	L/W
Terrapene	20.625 $\pm$ 0.175	12.625 $\pm$ 0.260	260.39	1.63
Chrysemys	20.625 $\pm$ 0.362	14.375 $\pm$ 0.194	296.48	1.44
Pseudemys	20.125 $\pm$ 0.133	10.625 $\pm$ 0.119	213.83	1.89
Chelydra	22.125 $\pm$ 0.199	14.750 $\pm$ 0.252	326.35	1.50

TABLE 2.—Comparison of blood values of turtles

Species	Erythrocyte count (number cell/mm <sup>3</sup> )	Hematocrit (volume percent)	Hemoglobin (g/100 ml blood)	Specific gravity	pH
<i>Terrapene</i>	368,333 ± 17,700	24.9 ± 1.0	10.1 ± 0.6	1.019 ± 0.001	7.68 ± 0.12
<i>Chrysemys</i>	395,000 ± 15,200	27.5 ± 2.6	11.2 ± 0.5	1.020 ± 0.005	7.77 ± 0.004
<i>Pseudemys</i>	495,883 ± 53,300	35.0 ± 1.5	11.1 ± 1.1	1.021 ± 0.041	7.61 ± 0.50
<i>Chelydra</i>	154,166 ± 19,000	21.0 ± 1.4	12.3 ± 0.1	1.020 ± 0.029	7.60 ± 0.07

like *Terrapene* in its habits since it spends a great deal of time on land, table 3 presents data which when plotted as in fig. 1 is comparatively similar to that curve representing the oxygen curve of the blood of *Terrapene*. Again the percent oxygen saturation of the blood at 40 mm Hg pressure is around 82% which is almost the same as in *Terrapene*.

*Pseudemys*, on the other hand, presents a slight variation. At low pressures, that is, from 10 mm Hg pressure and below, there are indications of a sigmoid curve which is so characteristic of mammalian bloods.

The data for the oxygen dissociation curve of the *Chelydra* show something of an exception. From the data of table 3 and fig. 1, it can be seen that a very prominent sigmoid curve is exhibited by this blood. The 40 mm Hg mark falls about 10 units below the percentage of oxygen in the blood as found in the other species.

In reference to the dissociation curve for carbon dioxide there are a few factors to be noted. All the carbon dioxide curves are relatively similar. The low pressures of carbon dioxide all started at about 40 or 55 percent saturation in the bloods and a plateau effect was found at about the 50 mm Hg partial pressures. Table 3 shows that in the case of *Terrapene* there is a sudden rise as the pressures increase up to about 50 mm Hg partial pressure at which point the plateau at the 82 percent blood saturation level is evident. It is of interest to note that the carbon dioxide dissociation curve of *Terrapene* falls lower than that of any other species. Blood of *Chrysemys* shows a dissociation curve for carbon dioxide which appears to climb steadily. In table 3 a plateau is hinted at by the pressures of 59 and 70 mm Hg. It is evident that the blood of this species contains a greater percentage of carbon dioxide when compared with the curves of the bloods of the other species. *Pseudemys* has blood which shows a dissociation curve similar to that of the blood of *Chrysemys*.

#### DISCUSSION

Two major families of turtles were represented in this investigation. The species of *Terrapene*, *Chrysemys*, and *Pseudemys* are included in the family Emydidae, while the species of *Chelydra* is placed in the family, Chelydridae (Carr, 1952).

When the cell size is considered (table 1), it can be seen that this size is greatest for *Chelydra*. This figure of 326.35 is greater by 29.87 than that for the highest figure given in the other family by *Chrysemys*. The present investigation has found cells of the *Terrapene* to be 20x12 micra. Size and shape of erythrocytes are features of great importance in connection with the efficiency of corpuscles which must be transported quickly to every part of the organism. A comparison of cell size is available in the composite table

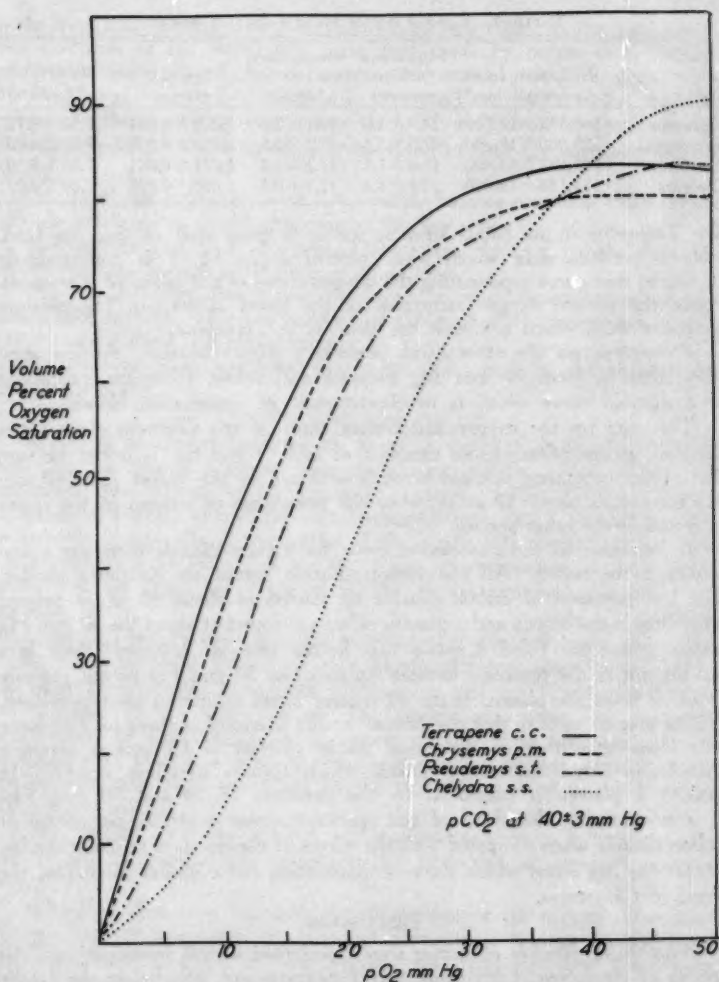


Fig. 1.—Graph showing comparison of the oxygen dissociation curves of four species of turtles.

given by Prosser *et al.* (1950). In that list, *Anguis fragilis* is the only reptile whose blood has cells anywhere near in size to that of the turtles. The size presented in these data is 17.8 micra by 9.3 micra. In the group of Amphibia, however, are many examples of large erythrocytes. For example, *Rana esculenta* has cells 22.8 x 15.7 micra; *Hyla arborea*, 18.5 x 11.7 micra; and *Bufo vulgaris*, 20.5 x 13.3 micra.



TABLE 3.—Gas analysis of blood of 12 individuals of each of four species of turtles. Equilibration at 25° C.

OXYGEN (CO <sub>2</sub> held at 40±3 mm Hg)		CARBON DIOXIDE (O <sub>2</sub> at air pressure)	
Partial pressure mm Hg	Percent saturation of blood	Partial pressure mm Hg	Percent saturation of blood
<i>Terrapene c. carolina</i>			
4	20	5	45
10	45	11	51
12	54	20	58
20	70	29	69
26	76	40	71
31	82	49	72
35	83	56	73
39	82	62	75
46	84	75	73
49	84	89	73
<i>Chrysemys picta marginata</i>			
5	22	5	55
12	46	10	62
17	61	17	68
20	70	20	72
23	75	31	75
32	80	37	80
35	82	50	82
40	82	59	84
47	85	70	84
50	82	80	88
		88	89
		90	89
<i>Pseudemys scripta troostii</i>			
6	12	5	43
10	30	11	60
13	50	17	65
19	60	21	68
24	71	30	68
31	76	42	74
36	80	49	76
40	82	59	80
45	85	68	82
50	86	72	82
		80	80
		91	83
<i>Chelydra serpentina serpentina</i>			
7	5	4	46
10	12	9	62
12	15	12	65
15	22	18	70
20	30	30	73
26	36	46	78
30	48	53	82
34	57	58	83
39	70	65	83
45	78	72	84
48	86	83	83
50	89	92	83

The hemoglobin content is the greatest in the blood of *Chelydra* (table 2). There is a gradual progression from 10.1 grams per hundred cubic centimeters in the blood of *Terrapene* to 12.3 grams per hundred cubic centimeters in the case of *Chelydra*. Dill and Edwards (1935) present an interesting comparative set of data on the hemoglobin content of certain reptiles. For the *Crocodylus* they found 4.27 mM per liter, for the *Alligator*, 5.42; for *Heloderma*, 4.75 to 5.07; for *Sauromalus*, 4.43 to 5.17. *Anguis fragilis* (Prosser *et al.* 1950) is the reptile which has a blood picture nearest to that presented by the turtles. The figure of 11.3 grams per hundred cubic centimeters of cells is the figure given for the hemoglobin content of its blood. Altland (cited by Albritton, 1952) has found the hemoglobin value of *Terrapene* to range between 6.1 and 9.1 grams per hundred cubic centimeters of blood. This investigation found it to be 10.1 grams per hundred cubic centimeters of blood.

The striking similarity in the values for the pH of the bloods is not surprising. An example of similarities in the pH of bloods is presented by Redfield (1933). His figure for *Chelydra* is 7.60 which is exactly what was determined in this study. Further evidence of the close similarity in the pH of bloods of reptiles is presented by Dill and Edwards (1935). Their data on pH are as follows: *Alligator*, 7.61; *Heloderma*, 7.40; *Sauromalus*, 7.52. It is evident that the alligator compares in pH range most nearly to that of the turtle group while the other mentioned figures are somewhat lower.

In reference to the specific gravities of the bloods of turtles in this investigation, there is some variation to be noted. The range of 1.019 to 1.021 as arrived at in this investigation is lower than the figure arrived at by Burton-Opitz (1902) on the blood of *Clemmys insculpta* who found the figure to be 1.0358. Lack of other data of this nature prevents any valid speculation or comparison of this factor in the Reptilia.

Hematocrit values are very similar for all the species considered. Apparently the increase in the size of the cells of the blood of *Chelydra* is sufficient to compensate for its decrease in numbers so far as cell volume is concerned. A similarity in results of this investigation and that of Altland is very evident (cited by Albritton, 1952). Altland found there to be 25 volume percent cells which is the same figure which was arrived at in this study, it being 24.9 (table 2).

An especially interesting picture is to be gained from the data on the erythrocyte number. *Chelydra* has the smallest number of cells with 154,166 cells per cubic millimeter of blood (table 2). The other three species, namely, *Terrapene*, *Chrysemys*, and *Pseudemys* have counts which are somewhat higher than that of *Chelydra*, yet which are very similar to each other. They are 368,333, 395,000, and 495,883 respectively (table 2). Extreme care must be taken in the interpretation of these data; at best, only a speculation can be presented. Considering first the evolutionary possibility, *Chelydra* with its low red cell number, high hemoglobin content, and large cell size belongs to the family Chelydridae. *Terrapene*, *Chrysemys*, and *Pseudemys* with their high cell numbers, relatively low hemoglobin contents, and smaller cell sizes belong to the family Emydidae. Perhaps there is a possibility that the blood of Chelydridae is more primitive and hence presents a different picture

chemically. This is also suggested by the comparisons of the oxygen dissociation curves as given graphically in fig. 1.

The oxygen affinity of the hemoglobin of the bloods of the reptiles varies. With the exception of *Chelydra*, the change in position of the curves from left to right (fig. 1) is accompanied by a slight increase toward the sigmoid shape. *Chelydra* blood curve does not follow the usual trend but shows a very exaggerated sigmoid shape. Also of interest is the fact that the three species of the family Emydidae all converge in the upper oxygen limits at around 40 mm Hg pressure with the blood being saturated at 82 percent with oxygen.

In reference to the great difference found between the curve of *Chelydra* and the curves of the other species considered, one can consider several possibilities. First, the hemopoetic apparatus of the two families may differ greatly. Second, the activity of these animals is known to differ and may make for a great difference in the metabolic activities and hence the individual cellular requirements would differ. *Chelydra* which is considered the most pugnacious and the greatest swimmer of the animals studied might require a greater concentration of oxygen released at a higher pressure. Contrasted with this is *Terrapene* which is wholly terrestrial, and which closes its shell and awaits the passing of its enemy. It does not show any tendencies to put up a fight. This variance in activity would suggest a difference in the individual demand for oxygen and hence the manifestation of a different dissociation curve.

Table 3 shows the results obtained in this experiment to determine the ability of the blood of turtles to transport carbon dioxide. Somewhat similar results were evident in all cases. When compared with other animals, as Redfield (1933) has done, it is of note that turtle blood has a relatively greater concentration of carbon dioxide. In view of the fact that this turtle group has a relatively smaller number of erythrocytes than have the other animals, the carbon dioxide must be contained primarily in the plasma, thus distributing it through a large volume. The buffering which is controlled primarily by the hemoglobin in the mammalian group is of necessity taken over by the plasma in this group of representatives from the reptilian group. From the investigations on *Pseudemys* by Southworth and Redfield (1926), it is evident that the amount of bicarbonate in turtle blood is exceptionally high as compared with that of the blood of man. This is a rather natural condition since the excess cations that might be free in the plasma, as a result of the carbon dioxide being contained there, can consequently combine with the carbonic acid to form the bicarbonates.

Representative samples of blood from both sexes of turtles were studied and no sexual differences in relation to the factors discussed here were noted.

From the observations made here, it is evident that there is a great need for more data on the hematology of representatives of the reptilian groups.

#### SUMMARY

An investigation was made of the bloods of four species of turtles, namely, *Terrapene c. carolina*, *Chrysemys picta marginata*, *Pseudemys scripta troostii*, and *Chelydra s. serpentina*.

*Chelydra* was found to have the fewest red blood cells with only 154,166

per cubic mm, while the other species had cells ranging in number from 368,333 to 495,883 per cubic mm.

*Chelydra* was found to have the largest size red blood corpuscles of any of the species studied.

A gradual progression from 10.1 grams per hundred milliliters of blood to 12.3 grams per hundred milliliters of blood ranging from *Terrapene* through *Chrysemys*, *Pseudemys*, and *Chelydra* was found as the hemoglobin value.

Hematocrit values were similar for all the bloods examined.

Oxygen dissociation curves of the bloods also differed greatly, ranging from the hyperbolic, fetal-like type of *Terrapene* through gradations to the positively sigmoid shape of the curve presented by the blood of *Chelydra*.

Carbon dioxide dissociation curves were all very similar. When compared with the blood of other animals, that of the turtle was shown to have a greater concentration of carbon dioxide which was believed to be in the plasma.

The specific gravity of the blood of all the individuals studied was very similar. The figure averaged around 1.020.

It is shown that some of the blood characteristics such as the oxygen dissociation curves are related to the activity of the species.

#### REFERENCES

- ALBRITTON, E. C. 1952—Standard values in blood. Philadelphia: Saunders.
- BOCK, A. V., H. FIELD, JR., AND G. S. ADAIR 1924—The oxygen and carbon dioxide dissociation curves of human blood. *J. Biol. Chem.* 59:353-378.
- BURTON-OPITZ, R. 1902—A comparative study of viscosity of the blood. *Amer. J. Physiol.* 7:243-260.
- CAGLE, FRED R. 1939—A system of marking turtles for future identification. *Copeia* 1939:170-173.
- CARR, ARCHIE 1952—Handbook of turtles. Cornell Univ. Press.
- CONSOLAZIO, C. F., R. E. JOHNSON, AND E. MAREK 1951—Metabolic Methods. St. Louis: C. V. Mosby Company.
- DILL, D. B. AND H. T. EDWARDS 1935—Properties of reptilian blood. IV. The alligator (*Alligator mississippiensis* Daudin). *J. Cell. Comp. Physiol.* 6:243-254.
- EVELYN, K. A. AND H. T. MALLOY 1938—Microdetermination of oxyhemoglobin, methemoglobin, and sulfhemoglobin in a single sample of blood. *J. Biol. Chem.* 126:655-662.
- HEPLER, O. E. 1950—Manual of clinical laboratory methods. Springfield, Illinois: Charles C. Thomas.
- PHILLIPS, R. A., D. D. VAN SLYKE, P. B. HAMILTON, V. P. DOLE, K. EMERSON, JR., AND R. M. ARCHIBALD 1950—Measurement of the specific gravities of whole blood and plasma by standard copper sulphate solutions. *J. Biol. Chem.* 183: 305-330.
- PROSSER, C. L., D. W. BISHOP, F. A. BROWN, JR., T. L. JAHN, AND V. J. WULF 1950—Comparative animal physiology. Philadelphia: Saunders.
- REDFIELD, A. C. 1933—The evolution of the respiratory function of the blood. *Quart. Rev. Biol.* 8:31-57.
- SOUTHWORTH, F. C. AND A. C. REDFIELD 1926—The transport of gas by the blood of the turtle. *J. Gen. Physiol.* 9:387-403.
- TIPTON, S. R. 1933—Factors affecting the respiration of vertebrate red blood cells. *J. Cell. Comp. Physiol.* 3:313-340.
- VAN SLYKE, D. D. AND J. M. NEILL 1924—The determination of gases in blood and other solutions by vacuum extraction and manometric measurements. *J. Biol. Chem.* 61:523-573.
- WINTROBE, M. M. 1933—Variations in size and hemoglobin content of erythrocytes in the blood of various vertebrates. *Folia Haematologica* 51:32-36.

# A Distributional Summary of the Herpetofauna of Indiana and Illinois

Philip W. Smith

*Illinois Natural History Survey, Urbana*

Sherman A. Minton, Jr.

*Indiana University Medical Center, Indianapolis*

Our recent independent studies of the amphibians and reptiles of Illinois and Indiana have led to the accumulation of a great many locality records, so that the ranges of many species in these states may be plotted with some confidence. In summarizing our ecological and zoogeographic data, we discovered independently certain interesting correlations that might be of greater value if published jointly rather than buried in our respective herpetofaunal reports.

Ninety-seven species of amphibians and reptiles are known to occur in Indiana and Illinois, and 77 species have ranges terminating within one or both states. The range limits of 75 of these species\* have been plotted on a series of base maps. Each line indicating the edge of a range bears a number corresponding to a species number in the accompanying table. In a few cases, the range edges of species are not aligned at the Illinois-Indiana border. When this happens, it is assumed that (1) there has been insufficient collecting in the border area, (2) local modification by human activity has eradicated the species before scientific record was made of its presence, (3) an erroneous published record or a specimen with incorrect locality data has inadvertently been included, (4) there is an abrupt ecological change coinciding with the political boundary.

The grouping of range edges on the maps has been dictated by the ecological relationships of the species, the general similarity of distributional patterns, convenience of graphic representation, and, in a few cases, by our inability to categorize the distribution. The primary divisions into northern, southern, eastern, and western components are to some extent arbitrary and subjective. For example, the approximate geographic center of the range of *Sistrurus catenatus* is west of our area, but we regard the species as northern because it behaves as such within our geographic area. Contrariwise, we have chosen to regard *Desmognathus fuscus* as an eastern element, although its distribution within Indiana and Illinois is actually more suggestive of a southern component. Some physiographic and edaphic features that will be mentioned subsequently are shown in fig. 1.

## NORTHERN SPECIES

Ten species are included in this group. The most striking trend illustrated by their ranges is one of fragmentation with numerous isolated populations occurring to the south of the continuous ranges. This trend suggests a

\* *Bufo americanus* and *Graptemys pseudogeographica* have been omitted from this paper because of unsolved taxonomic problems affecting the forms in this area.



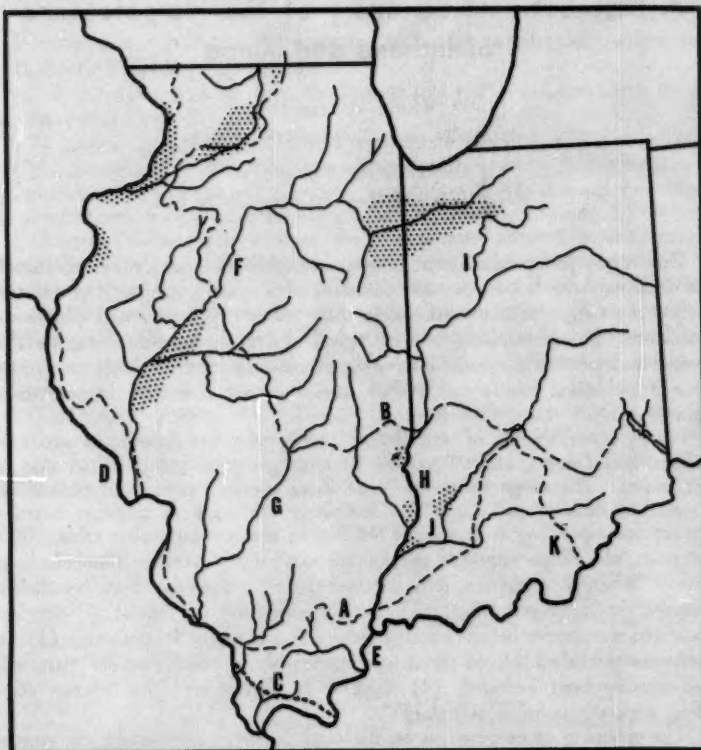


Fig. 1.—Stipple, major sand prairies: A. Illinoian glacial maximum; B. Wisconsin glacial maximum; C. Coastal Plain boundary; D. Mississippi River; E. Ohio River; F. Illinois River; G. Kaskaskia River; H. Wabash River; I. Tippecanoe River; J. White River; K. Knobstone Escarpment.

formerly more southern distribution. While human modification of habitats cannot be wholly discounted in production of this fragmentation of range, there is reason to believe the recession to the north was well advanced in pre-Columbian times.

The species are divisible into two groups. The first consists of five species characteristic of the humid tall grass prairie. The species and the numbers assigned to them in fig. 2 are:

<i>Emys blandingi</i>	1	<i>Elaphe vulpina</i>	4
<i>Thamnophis radix</i>	2	<i>Sistrurus catenatus</i>	5
<i>Opheodrys vernalis</i>	3		

Although these animals are essentially marsh or muck prairie inhabitants, they are not restricted to this habitat. Most of them occur also on sand prairies, on the light soils of prairie outliers, and on the heavier soils of the

Wisconsin glacial till. None is a forest animal within our area, although some, particularly *Sistrurus catenatus*, may be forest-edge species.

The second group of species and the numbers assigned to them in fig. 3 are:

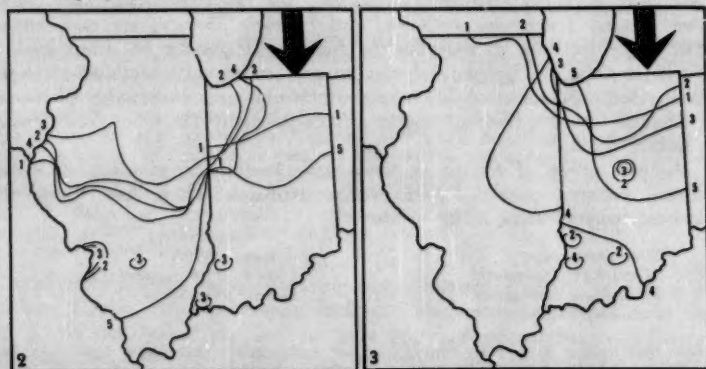
<i>Ambystoma laterale</i>	1	<i>Natrix kirtlandi</i>	4
<i>Hemidactylum scutatum</i>	2	<i>Thamnophis butleri</i>	5
<i>Clemmys guttata</i>	3		

*Ambystoma laterale*, *Hemidactylum scutatum*, and *Clemmys guttata* are species of bogs or cool, damp forest and are generally distributed through the Indiana lake plains and extreme northeastern Illinois. The latter two are known as rare bog relicts in the central Indiana till plains. *Natrix kirtlandi* and *Thamnophis butleri* are cold tolerant, damp grassland species that may have been early post-Wisconsin immigrants. Their decidedly sporadic occurrence today may reflect deterioration of their habitat through ecological succession. *Thamnophis butleri* seems well on the way to extinction within our area, being known from only five widely separated localities. Civilization has tended to preserve *Natrix kirtlandi*, for the great majority of known localities are urban or suburban vacant lot populations.

#### SOUTHERN SPECIES

In this category, we recognize thirty-one species and four groups. The first of these consists of 11 forest or forest-edge species that reach the northern limit of their range in Indiana and Illinois at or near the Shelbyville Moraine which marks the southernmost limit of Wisconsin glaciation. These species and the numbers assigned to them in fig. 4 are:

<i>Plethodon glutinosus</i>	1	<i>Haldea valeriae</i>	7
<i>Eurycea longicauda</i>	2	<i>Opheodrys aestivus</i>	8
<i>Sceloporus undulatus</i>	3	<i>Lampropeltis getulus</i>	9
<i>Scincella laterale</i>	4	<i>Ancistrodon contortrix</i>	10
<i>Eumeces laticeps</i>	5	<i>Crotalus horridus</i>	11
<i>Carpophis amoenus</i>	6		



Figs. 2, 3.—Range edge patterns of northern species. Western component: 1) *Emys blandingi*; 2) *Thamnophis radix*; 3) *Opheodrys vernalis*; 4) *Elaphe vulpina*; 5) *Sistrurus catenatus*. 3. Eastern component: 1) *Ambystoma laterale*; 2) *Hemidactylum scutatum*; 3) *Clemmys guttata*; 4) *Natrix kirtlandi*; 5) *Thamnophis butleri*.

Absence of relict populations and lack of other evidence indicating gross range fragmentation suggests that these species are extending their local ranges where habitat permits or that they were doing so until extirpated through human agency. A feature seen in the ranges of most of these forms is extension into rocky bluff habitats along the Illinois and Mississippi rivers and into the Turkey Run-Shades area of west-central Indiana.

Several other noteworthy trends are shown in fig. 4. Most of these species tend to avoid the swampy valley of the lower Wabash. This is obvious in the case of *Sceloporus undulatus* and *Eurycea longicauda*. Some other species, e.g. *Crotalus horridus*, *Ancistrodon contortrix*, occur within the valley only on bluffs or other islands of high ground. *Eurycea longicauda* and *Carphophis amoena* have ranges terminating well south of the Shelbyville Moraine in Illinois, probably because the requisite rock outcrop habitat is lacking. Three species, *Scincella laterale*, *Haldea valeriae*, and *Lampropeltis getulus*, are not recorded more than a few miles east of the Knobstone Escarpment which more or less marks the eastern boundary of the southern Indiana unglaciated plateau. All three species appear again in the unglaciated section of south-central Ohio, and all occur northward to the Shelbyville Moraine in Illinois.

A second group of nine austroriparian species enters our area chiefly in the region immediately surrounding the confluence of the Mississippi and Ohio rivers. These species and the numbers assigned to them in fig. 5 are:

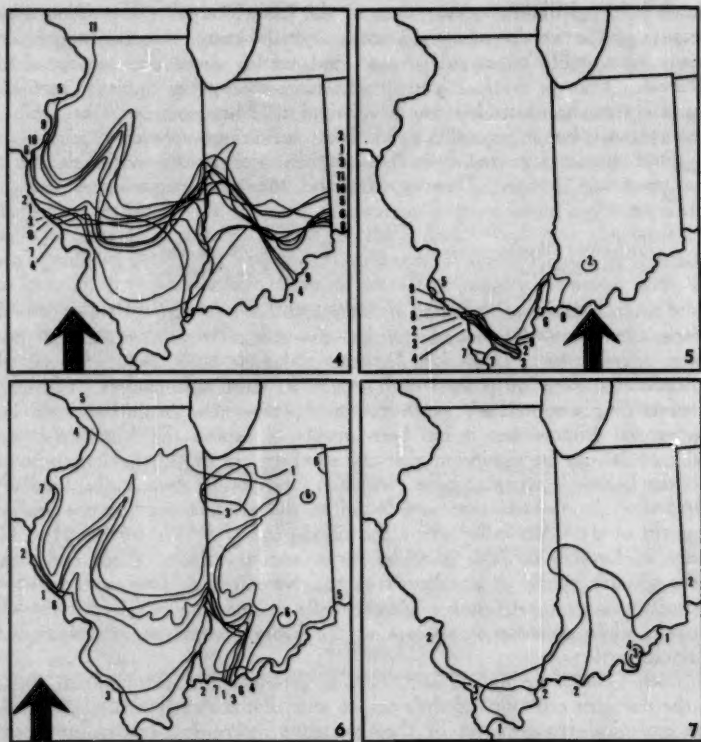
<i>Ambystoma talpoideum</i>	1	<i>Pseudemys floridana</i>	6
<i>Scaphiopus holbrooki</i>	2	<i>Natrix cyclopion</i>	7
<i>Hyla arivoca</i>	3	<i>Farancia abacura</i>	8
<i>Hyla cinerea</i>	4	<i>Ancistrodon piscivorus</i>	9
<i>Microhyla carolinensis</i>	5		

These are primarily swamp or floodplain forest species, although *Scaphiopus holbrooki* and *Microhyla carolinensis* also occur on savannas. Nearly all these species are sharply restricted to extreme southwestern Illinois. Only *Pseudemys floridana* extends eastward into the lower Wabash valley. Two other species, *Scaphiopus holbrooki* and *Farancia abacura*, are each known from single localities in southwestern Indiana. It cannot be determined at present if these are isolated colonies or part of recently continuous ranges. Small relict populations of *Microhyla carolinensis* and *Ancistrodon piscivorus* in Monroe County, Illinois, suggest a more northerly range for these species in former times.

A third group of aquatic or semiaquatic southern species exhibits distributional patterns correlated with stream drainage. These species and the numbers assigned them in fig. 6 are:

<i>Siren intermedia</i>	1	<i>Trionyx muticus</i>	5
<i>Macrochelys temminckii</i>	2	<i>Natrix erythrogaster</i>	6
<i>Kinosternon subrubrum</i>	3	<i>Natrix rhombifera</i>	7
<i>Pseudemys scripta</i>	4		

*Siren intermedia* and *Pseudemys scripta* have fairly extensive ranges along the major rivers of central Illinois and in the lakes of northern Indiana, especially those associated with the Kankakee and Tippecanoe river systems. Both these species are characteristic of the shallow, warm, quiet water of ponds and sloughs where aquatic vegetation is plentiful. *Kinosternon subrubrum* has



Figs. 4-7.—Range edge patterns of southern species. 4. Shelbyville moraine component: 1) *Plethodon glutinosus*; 2) *Eurycea longicauda*; 3) *Sceloporus undulatus*; 4) *Scincella lateralis*; 5) *Eumeces laticeps*; 6) *Carphophis amoenus*; 7) *Haldea valeriae*; 8) *Opheotryx aestivus*; 9) *Lampropeltis getulus*; 10) *Ancistrodon contortrix*; 11) *Crotalus horridus*. 5. Austroriparian component: 1) *Ambystoma talpoideum*; 2) *Scaphiopus holbrookii*; 3) *Hyla avivoca*; 4) *Hyla cinerea*; 5) *Microhyla carolinensis*; 6) *Pseudemys floridana*; 7) *Natrix cyclopion*; 8) *Parancia abacura*; 9) *Ancistrodon piscivorus*. 6. Fluvial component: 1) *Siren intermedia*; 2) *Macrochelys temminckii*; 3) *Kinosternon subrubrum*; 4) *Pseudemys scripta*; 5) *Trionyx muticus*; 6) *Natrix erythrogaster*; 7) *Natrix rhombifera*. 7. Otherwise uncategorized: 1) *Plethodon dorsalis*; 2) *Eurycea lucifuga*; 3) *Cemophora dolata*; 4) *Tantilla coronata*.

an apparently disjunct range, occurring in northwestern Indiana as well as in southern Illinois and southwestern Indiana. The northern population in the ponds and marshes of the Indiana sand prairie seems to be an ecological equivalent of *Kinosternon flavescens* of the Illinois sand prairie. *Natrix erythrogaster* also has a relict distribution, occurring sporadically in swamp forest in western Ohio, southern Michigan, and central Indiana and continuously in the lower Wabash, Ohio, and Mississippi valleys. *Macrochelys temminckii* and *Natrix rhombifera* have considerably more extensive ranges in

the Mississippi-Illinois system than in the Ohio-Wabash. The Ohio River, because of the scarcity of bayous and marginal swamp, becomes progressively more inhospitable to aquatic snakes and turtles above the mouth of the Wabash. *Trionyx muticus*, perhaps the most thoroughly fluviatile reptile of the midwest, has ascended the Mississippi to Minnesota and the Ohio to Pennsylvania, but it generally avoids lakes and minor streams.

Four species regarded by us as southern do not fit well with any of the preceding groups. These species and the numbers assigned them in fig. 7 are:

<i>Plethodon dorsalis</i>	1	<i>Cemophora doliata</i>	3
<i>Eurycea lucifuga</i>	2	<i>Tantilla coronata</i>	4

The salamanders, *Plethodon dorsalis* and *Eurycea lucifuga*, appear to be species that have differentiated within the ranges they now occupy. Both seem adapted to a troglodytic habitat, although they show little of the specialization seen in other North American cave salamanders. *Plethodon dorsalis* ranges appreciably northwest of the cave zone in Indiana and into east-central Illinois, but it has been unable to exploit the Mississippi bluff habitat. It may be significant that the southern tip of this habitat in southwestern Illinois is occupied by a *Plethodon cinereus*-like salamander. Similarly, *Plethodon dorsalis* has not been found in the extreme northeastern Indiana segment of the Ohio valley where the allied *Plethodon richmondi* occurs. The range of *Eurycea lucifuga* coincides better with the limits of the cave zone, although this species is not restricted to cave habitats. One is tempted to speculate that competition for a niche chiefly limits the range of *Plethodon dorsalis* while presence or absence of the niche governs the distribution of *Eurycea lucifuga*.

Both *Cemophora doliata* and *Tantilla coronata* are austroriparian species at the northern extremity of their ranges west of the Appalachians. Although the ecological requirements of these secretive, burrowing species are poorly known, both are considered relicts in Indiana and Illinois.

#### EASTERN SPECIES

Eighteen species have ranges situated predominantly to the east of Indiana and Illinois. Their range edges may be likened to a series of waves impinging upon the central Illinois prairie. For graphic clarity, the species have been arbitrarily divided into two groups. Those of the first group and the numbers assigned them in fig. 8 are:

<i>Diemictylus viridescens</i>	1	<i>Eumeces fasciatus</i>	5
<i>Rana clamitans</i>	2	<i>Storeria occipitomaculata</i>	6
<i>Rana palustris</i>	3	<i>Diadophis punctatus</i>	7
<i>Rana sylvatica</i>	4	<i>Elaphe obsoleta</i>	8

Most of these species are generally distributed over the originally forested portions of Indiana and are absent from the prairie of northwestern Indiana and central Illinois. Some such as *Rana clamitans*, *R. palustris*, and *Elaphe obsoleta* have continuous populations encircling major prairie areas uninhabited by them. Others such as *Diemictylus viridescens*, *Rana sylvatica*, and



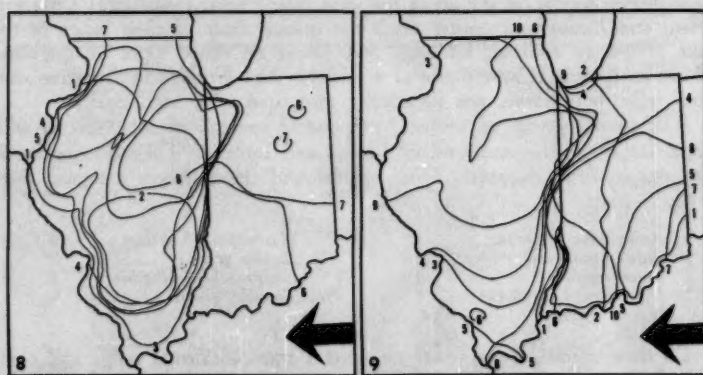
*Eumeces fasciatus* encroach on the predominantly prairie landscape where local conditions are favorable, particularly along river forest. Natural relict populations are unknown for most of these species, thus a fauna advancing with the last stage of forest succession is suggested.

Two cases deserve special comment. *Storeria occipitomaculata*, a woodland snake, is absent or excessively rare in the northern half and eastern third of Indiana and western half of Ohio. It is widely distributed, although uncommon, throughout Illinois and southwestern Indiana. This anomaly is not readily explained, for the reduced forest in Illinois would seem to provide the least amount of suitable habitat for the species. *Diadophis punctatus* also is a woodland snake that fails to utilize much of the available forest habitat in Indiana, for the northern limit of its range roughly coincides with the Shelbyville Moraine rather than with the cessation of forest. Both these snakes occur widely both to the north and to the south of Indiana and Illinois. They may represent elements of an earlier forest fauna partly obliterated in our area by a subsequent eastward extension of grassland.

The second group of eastern components and the numbers assigned them in fig. 9 are:

<i>Cryptobranchus alleganiensis</i>	1	<i>Plethodon cinereus</i>	6
<i>Ambystoma jeffersonianum</i>	2	<i>Plethodon richmondi</i>	7
<i>Ambystoma maculatum</i>	3	<i>Eurycea bislineata</i>	8
<i>Ambystoma opacum</i>	4	<i>Terrapene carolina</i>	9
<i>Desmognathus fuscus</i>	5	<i>Natrix septemvittata</i>	10

These species also occupy much of the originally forested portions of Indiana and Illinois, although a number have ranges terminating short of the present forest-prairie boundary. *Cryptobranchus* clearly represents a unique



Figs. 8, 9.—Range edge patterns of Eastern Species. 8. First group: 1) *Diemictylus viridescens*; 2) *Rana clamitans*; 3) *Rana palustris*; 4) *Rana sylvatica*; 5) *Eumeces fasciatus*; 6) *Storeria occipitomaculata*; 7) *Diadophis punctatus*; 8) *Elaphe obsoleta*. 9. Second group: 1) *Cryptobranchus alleganiensis*; 2) *Ambystoma jeffersonianum*; 3) *Ambystoma maculatum*; 4) *Ambystoma opacum*; 5) *Desmognathus fuscus*; 6) *Plethodon cinereus*; 7) *Plethodon richmondi*; 8) *Eurycea bislineata*; 9) *Terrapene carolina*; 10) *Natrix septemvittata*.

pattern associated with a specific fluviatile habitat. This wholly aquatic, rocky stream animal is known in our region only from the Ohio and lower Wabash valleys. Its range is undergoing rapid shrinkage as a result of human modification of stream habitats.

Disjunct populations of *Ambystoma opacum* at the southern tip of Lake Michigan and *Plethodon cinereus* at Pine Hills in extreme southwestern Illinois indicate that formerly more extensive ranges of these species once encompassed the sites of these relicts. Another distributional peculiarity is shown by *Desmognathus fuscus* which is plentiful in the southeastern quarter of Indiana, becomes rare and restricted to springs along the western edge of the Indiana unglaciated plateau, and appears again in a few sites in extreme southern Illinois.

#### WESTERN SPECIES

Sixteen species have ranges situated predominantly west of the Mississippi River and extend eastward into Illinois and Indiana. These species are divisible into two groups. Seven species have conspicuously disjunct populations suggesting that they are in the process of withdrawal from more extensive ranges in the east. These species and the numbers assigned them in fig 10 are:

<i>Pseudacris streckeri</i>	1	<i>Tropidoclonion lineatum</i>	5
<i>Kinosternon flavescens</i>	2	<i>Heterodon nasicus</i>	6
<i>Terrapene ornata</i>	3	<i>Pituophis catenifer</i>	7
<i>Cnemidophorus sexlineatus</i>	4		

Six of the above species have populations conspicuously associated with sand prairies. In fact, the relict colonies of *Pseudacris streckeri*, *Kinosternon flavescens*, and *Heterodon nasicus* are restricted to certain sand areas, and these species do not occupy all of the sand prairie habitat available. *Terrapene ornata* and *Pituophis catenifer* reach the eastern limit of their range in the sand prairie of Indiana, although they occur on other types of grassland habitat in Illinois. *Cnemidophorus sexlineatus* and *Tropidoclonion* have scattered relict populations not necessarily associated with sand prairie.

The second group of western components consists of nine species with ranges largely to the southwest of Illinois and Indiana. Their distribution is not conspicuously disjunct. These species and the numbers assigned them in fig. 11 are:

<i>Ambystoma texanum</i>	1	<i>Masticophis flagellum</i>	6
<i>Bufo woodhousei</i>	2	<i>Elaphe guttata</i>	7
<i>Rana areolata</i>	3	<i>Lampropeltis calligaster</i>	8
<i>Ophisaurus attenuatus</i>	4	<i>Tantilla gracilis</i>	9
<i>Natrix grahami</i>	5		

Of these species, *Bufo woodhousei* has a transcontinental range and obviously has very wide ecological tolerance. *Ambystoma texanum* also exhibits considerable adaptability. It ranges completely across Indiana and Illinois and occupies diverse habitats including dense forest as well as intensively farmed areas. At the other extreme, *Masticophis flagellum*, *Elaphe guttata*, and *Tantilla gracilis* enter our region only in a very restricted area of hill prairie and adjacent forest-edge along the Mississippi River in southwestern Illinois. The ranges of the remaining species terminate at various places

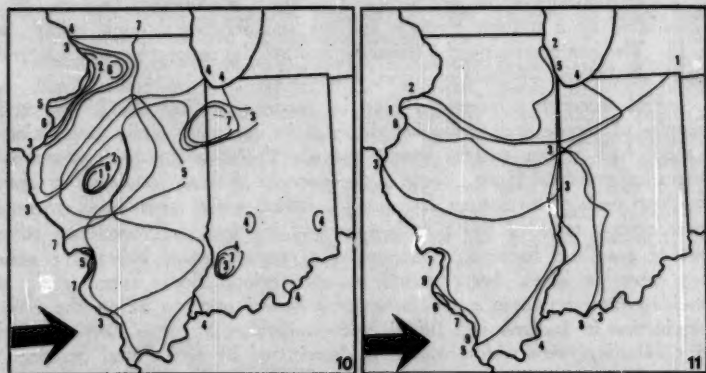
within the prairie-forest ecotone. *Ophisaurus attenuatus* is peculiar in that it penetrates a considerable distance eastward in the sand region of northwestern Indiana, although its distribution in Illinois seems unrelated to the existence of sand prairie. Six of the nine species in this group are known from the "barrens" or patches of relict prairie in central Kentucky.

#### ECOLOGICAL AND ZOOGEOGRAPHIC INFERENCES

In the case of weakly vagile animals such as amphibians and reptiles, the composition of the fauna in a given area is profoundly influenced by the ecological tolerances of the species, the diversity of habitats available, and the ecological history of the region. If the distributional maps on the preceding pages are superimposed, several instances of zonation or coincidence of range edges are evident. Conversely, certain parts of our area appear to be rather uniform ecologically as the range edges exhibit a shingling effect, suggesting a gradual ecotone rather than an abrupt change.

The most prominent zonation of range edges occurs where a prairie landscape abruptly replaces the deciduous forest and involves predominantly eastern and western species. The coincidence is notable in extreme northwestern Indiana, at about the Indiana-Illinois state line, and along the Mississippi River where gallery forest suddenly replaces prairie. In the Wabash valley an ecotone consisting of interdigitating forest and prairie occurs, and the coincidence of range edges is less pronounced. A tendency for the ranges of eastern species to circumvent the central prairie region of Illinois and to ascend and descent the forested valleys and bluffs of the Illinois and Mississippi rivers is clearly evident.

The replacement of eastern by western components in areas where forest is replaced by prairie is illustrated by three transects across Illinois and



Figs. 10, 11.—Range edge patterns of western species. 10. Relict component: 1) *Pseudacris streckeri*; 2) *Kinosternon flavescens*; 3) *Terrapene ornata*; 4) *Cnemidophorus sexlineatus*; 5) *Tropidoclonion lineatum*; 6) *Heterodon nasicus*; 7) *Pituophis catenifer*. 11. Southwestern component: 1) *Ambystoma texanum*; 2) *Bufo woodhousei*; 3) *Rana areolata*; 4) *Ophisaurus attenuatus*; 5) *Natrix grahami*; 6) *Masticophis flagellum*; 7) *Elaphe guttata*; 8) *Lampropeltis calligaster*; 9) *Tantilla gracilis*.

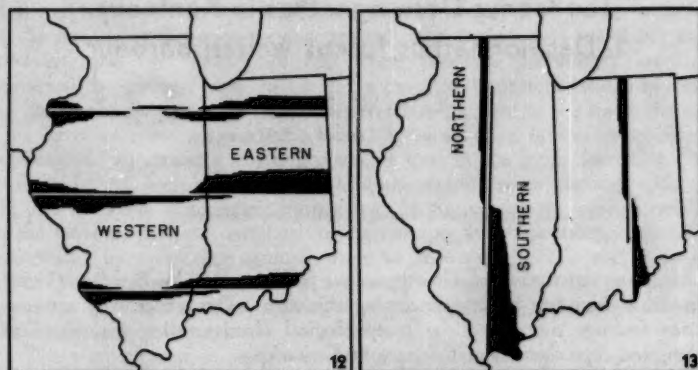
Indiana in fig. 12. The uppermost transect traverses some marginal forest and sand prairie along the Mississippi River, the prairie between the Mississippi and Illinois rivers, the forested Illinois River valley, the sandy prairies of northeastern Illinois and northwest Indiana, and the originally forested eastern half of Indiana. An examination of the bar graphs along this transect reveals that the ranges of eastern and western elements tend to be mirror images of each other. The middle transect crosses the interdigitating forest and prairie between the Mississippi and lower Illinois rivers, the sand prairie on the east side of the Illinois River, the central Illinois muck prairie, the Turkey Run-Shades area in western Indiana, and the forest of central Indiana. The most prominent features of this transect are the ecological distinctiveness of the sand prairies and the sharp replacement of western species by an eastern fauna at the forest-prairie border. The lowermost transect runs through an area of intermingled forest and hill prairie along the Mississippi River, the mixed forest and savanna of south-central Illinois, and the progressively richer and more mesic forest of southern Indiana. The most prominent features of the bar graphs along this transect are the proportionately high number of eastern components, compared with the two northern transects, and the gradual diminution of the eastern fauna within south-central Illinois.

Zonation is also prominent from north to south. The coincidence of range edges is most conspicuous at the Shelbyville Moraine, which marks the southern limit of Wisconsin glaciation, and at the northern edge of the austroriparian biotic province. Less prominent breaks are evident at the Shawnee Hills border in southern Illinois and Knobstone Escarpment in southern Indiana, both of which mark the southern limit of Illinoian glaciation. Other minor breaks are seen along the border of the Wabash lowland and the southern limit of Great Lakes Plains Section.

The relationship of the northern and southern components to each other is illustrated by a transect through Indiana and another through Illinois in fig. 13. The bar graphs on the transects indicate the geographic position and relative significance of these ecological boundaries.

Several interesting inferences may be made regarding the history and dynamics of reptile and amphibian dispersal in our area. Relict populations of about half of our western species provide almost irrefutable evidence of a retreating grassland fauna. Some of these species such as *Pseudacris streckeri* have been reduced to a very few small colonies, while others as *Terrapene ornata* occupy most of the available sand prairie and spill over into other types of grassland habitats. Evidence of a similar nature indicates a once more extensive boreal herpetofauna in our region. Some forms such as *Hemidactylium scutatum* and *Thamnophis butleri* seem to be on the verge of extinction in Indiana and Illinois while others as *Sistrurus catenatus* and *Emys blandingi* were widespread until deracinated by agricultural practices.

The range edge patterns shown by most of the eastern and several of the southern components of our total fauna would seem to indicate an advancing forest and forest-edge fauna. The few relict populations, the concentrically arranged limits of range, and the encroachment along forested river valleys and bluffs all convey the impression that these animals are actively extending their ranges westward into recently available forest habitats.



Figs. 12, 13.—12. East-West Transects across Illinois and Indiana at three levels showing replacement of eastern forest fauna by western prairie fauna. 13. North-South transects through Illinois and Indiana showing graphically the relative significance of the Shelbyville Moraine and other ecological boundaries in the distribution of northern and southern species.

A group of southern species, many of them clustered about the confluence of the Ohio and Mississippi rivers, appears to contrain relicts of a previous warm period. Some of their populations are in contact with the main body of the range in the south; others are disjunct. The northern ranges of some were quite extensive as shown by the presence of colonies of *Natrix erythrogaster* in southern Michigan and northwestern Ohio. The more aquatic species, *Siren intermedia*, *Pseudemys scripta*, and *Natrix rhombifera*, have been much more successful in dispersal than the fossorial *Ambystoma talpoideum*, *Microhyla carolinensis*, and *Cnemidophorus* *doliata*.

Tenuous evidence of an older, austral, midwestern herpetofauna is seen in the distributional patterns of *Storeria occipitomaculata* and *Diadophis punctatus*. These are forest animals whose ranges today extend from the Gulf Coastal Plain well into Canada. Both species have a range hiatus in northern Indiana and western Ohio that may have resulted from an eastward extension of prairie prior to the last stage of forest advance. There is also reason to think that *Plethodon cinereus*, *Natrix kirtlandi*, and *Thamnophis butleri* are early postglacial immigrants that have had a larger tenure in the midwest than the other species shown in figs. 2 and 3.



## The Genus *Desmognathus* in Kentucky I. *Desmognathus fuscus welteri* Barbour

Roger W. Barbour  
University of Kentucky, Lexington

Rodney M. Hays  
Transylvania College, Lexington, Kentucky

Since the description of *Desmognathus fuscus welteri* by Barbour (1950), there have been few papers concerning this race. This paper is a summary of our findings concerning the morphological characteristics, habitat, distribution, and reproduction of this race in Kentucky.

Almost all the literature records of *Desmognathus fuscus* in Kentucky are listed under *D. f. fuscus*, since the great majority of the publications antedate the description of *D. f. welteri*. In the following summary of the literature records, all, except where otherwise noted, were listed under *D. f. fuscus*.

Garman (1894) was apparently the first to record the species from the state with his Pulaski County record. Bishop (1926) listed the species from Breathitt County. Dunn (1926) examined specimens from Bell, Breathitt, Edmonson, Morgan, and Nelson counties. Pope (1928) recorded 104 specimens from Harlan County. Burt (1933) listed specimens from Bell, Cumberland, Estill, Harlan, Knott, Letcher, Metcalfe, Morgan, Perry, Pike, Rockcastle, Wayne, and Whitley counties. Dury and Williams (1933) took specimens from Breathitt, Carter, Harlan, Kenton, Laurel, and Woodford counties. Hibbard (1936) recorded the species from Mammoth Cave National Park Proposed, encompassing parts of Barren, Edmonson, and Warren counties. Welter and Carr (1939) reported specimens from Carter and Rowan counties. Adams (1939) mentioned specimens from the counties of Breathitt, Knott, Laurel, Lawrence, Leslie, Letcher, Magoffin, and Perry. Green (1941) reported specimens from Carter county. Barbour (*op. cit.*) examined specimens of *D. f. welteri* from Bath, Carter, Elliot, Harlan, Menifee, Pulaski, and Warren counties in Kentucky, and Wise county, Virginia. Barbour (1953) recorded a series of 761 individuals of *D. f. welteri* from Harlan county.

During the past fifteen years the senior author has accumulated a series of *D. fuscus* from Kentucky; all are currently deposited in the zoological collections of the University of Kentucky. They are from widespread localities in Kentucky, and all agree in most particulars with topotypical material of *D. f. welteri* from Harlan country. Apparently, *Desmognathus fuscus* is represented in Kentucky by a single subspecies, *D. f. welteri*.

Credit is due the Research Fund Committee of the University of Kentucky for financing numerous field trips in the last five years, and many individuals for assistance in collecting specimens.

The tedious chore of examining the specimens and recording data was done by the junior author.

The sex, snout-vent length, tail length, number of costal grooves, number

of costal folds between appressed toes, number of vomerine teeth, condition of the gonads in the females, and general color pattern was noted for each specimen, and the results tabulated where possible. Snout-vent length is defined as the distance from the tip of the snout to the posterior end of the vent; tail length the distance from the posterior end of the vent to the tip of the tail. This latter measurement was not taken if the tail was broken or obviously regenerated. In counting costal grooves, if that in the groin formed a "Y" with its fellow, both were counted. Vomerine teeth were counted with the aid of a binocular stereoscopic microscope. In the event eggs were discernible in the females, the total number was recorded as was their average diameter, determined by measuring at least three of the eggs. Totals and averages, where possible, were determined for each characteristic. In the case of vomerine teeth in the males, a strict average was avoided, because adult males frequently lack such teeth.

The method used in separating adults and juveniles was rather arbitrary. Each specimen was judged on the basis of size, color pattern, and the condition of the gonads. The presence of gills was always accepted as a juvenile character. Examination of numerous specimens revealed that on the average the juvenile characteristics disappeared by the time the animal reached a snout-vent length of 23 mm; hence, all specimens with a snout-vent length of 23 mm or more are considered adult.

#### MORPHOLOGICAL CHARACTERISTICS

*Desmognathus fuscus welteri* is a robust salamander, in both body and limbs. The snout is blunt and rounded, and widest in the region of the gular fold, where, in males, there may be a distinct swelling. The costal grooves are deep and prominent. There is a depressed median line down the back from the occipital region to a point over the vent. The tail may or may not bear a median keel; when present, the keel is usually indistinct.

The adult male exhibits a well developed mental gland, sufficiently distinct to enable one readily to separate the sexes. This gland is an elliptical elevation at the tip of the lower jaw, more prominent on older males.

The vomerine teeth are arranged in two short crescentic rows curving posteriorly from the lateral border of the internal nares. They are usually not joined to the parasphenoids. Occasionally a few of the vomerine teeth are so arranged as to form a partial second row. Young individuals and about one-half of the adult males are without vomerine teeth. All adult females normally have vomerine teeth. Each parasphenoid group is ovoid, being more slender anteriorly.

*Desmognathus f. welteri* is quite variable in pigmentation, but typically exhibits a tan to brown color dorsally with scattered, irregular black blotches. Usually there is no dorsal band. The belly is lighter than the dorsum, and rarely immaculate. The belly usually exhibits small black blotches which merge along the flanks with the more prominent dorsal blotches. These small ventral blotches give an overall mottled effect. In cases of extreme pigmentation, the belly is almost uniformly dark. The two areas of darkest ventral pigmentation are along the margin of the lower jaw and a transverse band between the gular fold and the origin of the fore limbs.

The snout-vent length of 885 adult males averaged 50.5 mm, with extremes of 23 and 89. Eight hundred and thirty-three females averaged 47 mm, with extremes of 23 and 72. Fig. 1, A and B, shows the frequency distribution of this measurement in males and females, respectively.

The average tail length in males was 45.7 mm, ranging from 16 to 76. In females, the average was 43 mm, ranging from 21 to 69.

In total length, males averaged 94.5 (39-165); females averaged 89 (44-134).

Ninety-two percent of the specimens had 14 costal grooves; a few had 12, 13, or 15. A "Y" was present in the groin of 84.6 percent of the specimens.

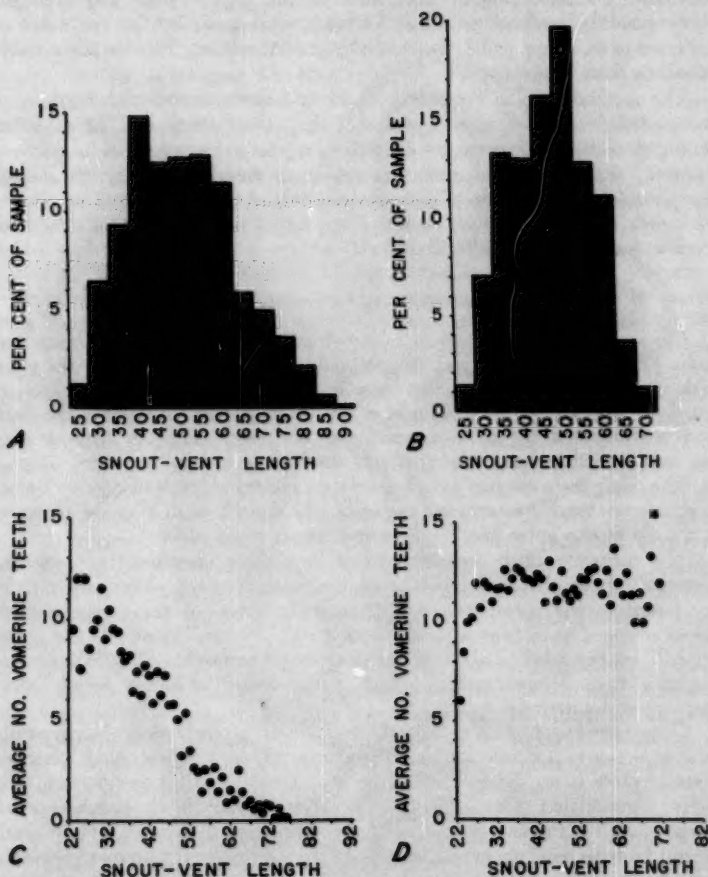


Fig. 1.—Snout-vent length and number of vomerine teeth in *Desmognathus fuscus welleri* from Kentucky. A. Frequency distribution in males; B. females. C. Number of vomerine teeth in relation to snout-vent length in males; D. females.

There was a definite correlation between the presence of the "Y" and the number of costal grooves. In those with 12 grooves, none had a "Y"; 13 grooves, 49% had it; 14 grooves, 90%; 15 grooves, 98%. There was no difference in the sexes in this respect.

The number of costal folds between appressed toes averaged 3.5, ranging from zero to six. No significant correlation between this character and sex of the specimens was observed. The most frequently observed number of costal folds between appressed toes was three, exhibited by 42 percent of the males and 39 percent of the females. The second most frequent number was four, exhibited by 24.5 percent of each sex.

Slightly over half (53.3 percent) of the adult males had vomerine teeth. The maximum number was 24; for those with teeth, the average was 8.5. The average for females was 12, ranging from zero to 15. There was frequently considerable variation in number of teeth from one side to the other in each sex.

It has long been known that adult males of *D. fuscus* lose their vomerine teeth (Dunn, *op. cit.*; Bishop, 1943). In an effort to determine at what size males generally lose their vomerine teeth, the relation between the number of vomerine teeth and snout-vent length was determined. In order to determine if any similar trend occurred in the females, a comparable study was made of this sex.

Usually males have lost their vomerine teeth by the time they attain a snout-vent length of 77 mm; there is apparently no loss of vomerine teeth with increasing snout-vent length in the females. These data are presented in fig. 1, C and D.

#### HABITAT

*Desmognathus f. welteri* is typically associated with mountain brooks, where the current is moderate to weak. A rocky woodland stream in Kentucky, with its banks well-littered with logs, dead leaves, and assorted debris almost always supports a large population. The species is frequently taken about permanent springs, most often under cover of some sort. Occasionally individuals are found under slabs of rock or vegetation adhering to the face of a cliff, but only in wet areas, as where a small stream trickles over the face of the cliff. They have occasionally been taken under stones in or near a stream flowing from a cave, but rarely beyond the lighted zone of the cave.

#### DISTRIBUTION IN KENTUCKY

This race occurs essentially throughout the state in suitable habitats; it reaches its maximum abundance in mountainous eastern Kentucky. We have examined no specimens from extreme western Kentucky, but Blanchard (1922) and Parker (1948) have listed the species from extreme western Tennessee (fig. 2).

#### REPRODUCTION

Eight hundred and twelve females were dissected in an effort to determine average egg number and diameter. Females were considered to contain ovarian eggs if the average egg diameter was one-half millimeter or more. Obviously this is an artificial distinction; this figure was selected as a minimum because

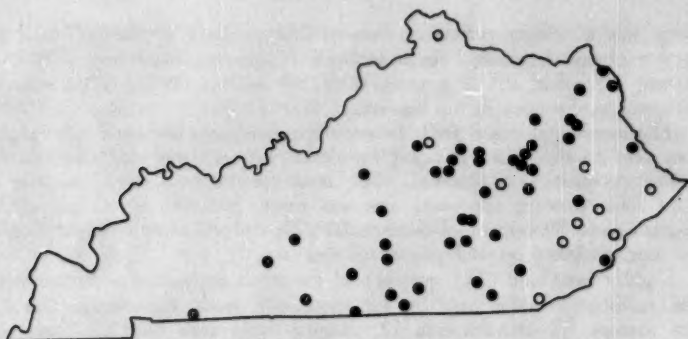


Fig. 2.—Distribution of *Desmognathus fuscus welteri* in Kentucky. Solid symbols represent specimens examined; hollow symbols literature records from counties from which no specimens were examined.

of the difficulty of counting smaller eggs without completely ruining the specimen. Three hundred and ninety seven of the females contained eggs.

Diameter of the eggs averaged 1.3 mm, varying from 0.5 to 3.0. Arrangement of the specimens by month collected (table I) reveals that the average egg diameter is remarkably constant throughout the year.

Wilder (1913), writing of *D. fusca*, reported the eggs laid as "numbering about 20 in all (15-20 according to Hilton), a number which corresponds in general also to the count of ripe eggs found in the ovaries of a large number of females which I have examined for comparison."

Dunn (*op. cit.*) stated that in *D. f. fuscus* the "females just matured at a length of 80 mm had usually 28 eggs in the ovaries, while larger females up to 100 mm had as many as 40 eggs."

Barbour (*op. cit.*) mentioned a cluster of 16 eggs of *D. f. welteri*, and reported the ovarian egg number of 45 females to average 27, varying from five to 39.

TABLE 1.—Total females taken, number with ovarian eggs, percent females with eggs, and average egg diameter in Kentucky *D. f. welteri*, by month collected.

	Total females	Females with eggs	Percent females with eggs	Average egg diameter
January	----	----	----	----
February	26	22	84.6	1.5
March	75	47	62.6	1.3
April	165	93	56.4	1.4
May	123	76	61.8	1.5
June	119	51	42.9	1.6
July	137	35	25.5	1.4
August	90	18	20.0	1.4
September	27	20	74.1	1.3
October	29	18	62.1	1.3
November	2	1	50.0	1.0
December	19	16	84.2	1.6



TABLE 2.—The relation of number of ovarian eggs to snout vent length in 393 *D. f. welteri*.

Snout-vent <sup>i</sup> length	Number females	Average egg number	Total eggs
30-34	12	11.6	139
35-39	20	13.9	278
40-44	41	17.1	701
45-49	91	22.9	2082
50-54	84	29.2	2449
55-59	67	30.2	2025
60-64	61	29.9	1823
65-69	13	30.2	392
70-74	4	37.0	148

In this study, the average egg number in 393 females was found to be 26, varying from two to 57. This strict average is misleading, however, because it was found that the average egg number varied with the size of the female (table II). No females with a snout-vent length of less than 30 mm contained ovarian eggs as large as one-half millimeter. Those with a snout-vent length of from 30 to 34 mm contained an average of 11.6 eggs; those from 35-39, 13.9; 40-44, 17.1; 45-49, 22.9; 50-54, 29.2. At about this point (i.e., a snout-vent length of about 55 mm), the average egg number became constant at about 30, regardless of the size of the female. There is some evidence that females over 70 mm contain more eggs, but too few specimens of this size were available to determine if such a conclusion is correct.

Wilder (*op. cit.*) and Bishop (*op. cit.*) agree that egg-laying in *D. f. fuscus* occurs in June, July, and August. Barbour (*op. cit.*) stated that in the case of *D. f. welteri* "apparently egg-laying continues throughout the summer." It may be expected that with the onset of egg-laying the number of egg-bearing females will decline in relation to the total female population. If eggs are deposited only in June, July, and August, this decline will appear at that time, and should be well-marked. Table 1 presents data relative to this decline; from these data one may infer that in Kentucky egg-laying begins in early March and continues at a steadily accelerating rate until a peak of egg-laying activity in August. At about the first of September a rapid decline sets in, and by December, the same percentage of females have ovarian eggs as was exhibited in February.

The fact that the percentage of females with eggs taken in March, April, and May is essentially constant should not be considered evidence of a cessation of an increase in the rate of egg-laying activity at this time. Those that lay eggs during this period are being replaced at a steadily increasing rate from the reservoir of females whose eggs were less than one-half a millimeter earlier in the year. By late May, this reservoir shows signs of depletion.

#### SUMMARY

One thousand seven hundred forty-three specimens of *Desmognathus fuscus welteri*, collected from 36 Kentucky counties were examined, and the literature pertinent to this species in the state surveyd.

Snout-vent length in males averaged 50.5 mm; in females, 47 mm. Tail length in males averaged 45.7, in females 43. Costal grooves varied from 12-15, with 92 percent of the population possessing 14. Number of costal folds between appressed toes averaged 3.5. In males possessing vomerine teeth, the number averaged 8.5; in females, 12. Males lost the vomerine teeth by the time they attained a snout-vent length of 77 mm. There was no loss of vomerine teeth with increasing size of the females.

This salamander is primarily terrestrial, but typically associated with mountain brooks and permanent springs. It occurs essentially throughout the state in suitable habitats, but reaches its greatest abundance in mountainous eastern Kentucky.

Average ovarian egg size was quite constant throughout the year. Average egg number of 393 females was 26, but there was definite correlation between snout-vent length and average egg number. Larger individuals contained more eggs, until a snout-vent length of approximately 55 mm was reached. At this point, average ovarian egg number leveled off at about 30; there is some indication that exceptionally large females contained more eggs.

Some individuals apparently lay their eggs as early as March. As the season progresses, more and more individuals deposit eggs until a peak of egg-laying activity is reached in August. There is apparently a rapid decline in egg-laying activity beginning about the first of September.

*Specimens examined.*—One thousand seven hundred forty three Kentucky specimens of *D. f. welteri* were examined, distributed by county as follows: ADAIR: 12 (Three miles south Columbia, 7; Coburg, 5); ALLEN: 13 (Scottsville, 13); ANDERSON: 30 (Tyrone, 30); BOYD: 11 (Pollard, 11); BREATHITT: 4 (Noble, 4); CARTER: 163 (Carter Caves, 163); CHRISTIAN: 5 (Fort Campbell, 5); CLARK: 21 (Oil Springs, 1; Hollywood, 6; Lower Howards Creek, 14); CLINTON: 6 (Albany, 6); CUMBERLAND: 6 (Eight miles east Burksville, 6); EDMONSON: 7 (Mammoth Cave, 7); ELLIOTT: 32 (Sandy Hook, 1; Ordinary, 31); FAYETTE: 1 (Grimes Mill, 1); GARRARD: 10 (Dix Dam, 10); GREENUP: 12 (Bellefonte, 12); HARLAN: 654 (Big Black Mountain, near Lynch, 654); JESSAMINE: 86 (Camp Daniel Boone, 63; Lock 9, Ky. River, 23); KNOX: 14 (Locality unknown, 14); LAUREL: 31 (Victory, 31); LEE: 10 (Beattyville, 10); MADISON: 179 (Boonesboro, 75; Big Hill, 104); MARION: 11 (Jessietown, 11); MARTIN: 2 (Inez, 2); MENIFEE: 57 (Red River Gorge, 55; Frenchburg, 2); METCALFE: 2 (Good Luck, 2); MONROE: 3 (Cyclone, 3); MORGAN: 19 (Wrigley, 19); NELSON: 25 (Bardstown, 25); POWELL: 71 (Natural Bridge State Park, 62; Nada, 9; PULASKI: 84 (Bandy, 1; Science Hill, 83); ROCKCASTLE: 6 (Mt. Vernon, 3; Brodhead, 3); ROWAN: 13 (Farmers, 13); WARREN: 48 (Two miles north Hadley, 48); WAYNE: 8 (Parnell, 8); WHITLEY: 64 (Williamsburg, 1; Cumberland Falls, 63); WOLFE: 23 (Tight Hollow, 23).

#### REFERENCES

- ADAMS, WILLIAM 1939—Some Amphibia of eastern Kentucky. M.S. Thesis, Geo. Peabody College for Teachers.
- BARBOUR, ROGER W. 1950—A new subspecies of the salamander, *Desmognathus fuscus*. *Copeia* (4):277-278.
- 1953—The amphibians of Big Black Mountain, Harlan county, Kentucky. *Ibid.* (2):84-89.
- BISHOP, SHERMAN 1926—Records of some amphibians and reptiles from Kentucky. *Ibid.* (152):118-120.
- 1943—Handbook of Salamanders. Comstock Publishing Co., Ithaca, N. Y.
- BLANCHARD, FRANK N. 1922—The amphibians and reptiles of western Tennessee. *Occ. Pap. Mus. Zool., Uni. Mich.* (117):1-18.

- BURT, CHAS. E. 1933—A contribution to the herpetology of Kentucky. *Amer. Midl. Nat.* 14(6):669-679.
- DUNN, EMMET REID 1926—The Salamanders of the Family Plethodontidae. Smith College, Northampton, Mass.
- DURY, RALPH, AND RAYMOND S. WILLIAMS 1933—Notes on some Kentucky amphibians and reptiles. *Bull. Baker-Hunt Foundation Mus.* 1:1-22.
- GARMAN, HARRISON 1894—A preliminary list of the vertebrate animals of Kentucky. *Bull. Essex Inst.* 26:1-63.
- GREEN, N. BAYARD 1941—The four-toed salamander in Kentucky. *Copeia* (1):53.
- HIBBARD, CLAUDE W. 1936—The amphibians and reptiles of Mammoth Cave National Park Proposed. *Trans. Kans. Acad. Sci.* 39:277-281.
- PARKER, MALCOLM V. 1948—A contribution to the herpetology of western Tennessee. *J. Tenn. Acad. Sci.* 22(1):20-30.
- POPE, CLIFFORD 1928—Some plethodontid salamanders from North Carolina and Kentucky with the description of a new race of *Leurognathus*. *Amer. Mus. Novit.* (306):1-19.
- WELTER, W. A. AND KATHERINE CARR 1939—Amphibians and reptiles of northeastern Kentucky. *Copeia* (3):128-130.
- WILDER, INEZ WHIPPLE 1913—The life history of *Desmognathus fusca*. *Biol. Bull.* 24(4):251-343.

## The Mating Behavior of Pionid Water-Mites

Rodger Mitchell

University of Vermont, Burlington

The striking modifications of the fourth leg of male Pionidae are assigned considerable importance as subfamily characters. It is also known that the species of each subfamily have a specific mating position and each has certain behavior traits as well (Piersig, 1900; Koenike, 1891; Viets, 1914; Motas, 1928; Marshall, 1929; Uchida, 1932, 1940). My observations verify the work of these authors and additional details of behavior are recorded below in order to make a detailed comparison of mating behavior in the two subfamilies that will contribute to an understanding of the relationships of the two groups.

Observations were made both in the field and on specimens kept in small containers in the laboratory. Although field observations were quite fragmentary they agree with laboratory studies and it is the latter that are discussed below unless otherwise stated. This work was carried out during the spring of 1954 at the Edwin S. George Reserve of the University of Michigan near Pinckney, Michigan, and was supported by a Grant-in-Aid from the Edwin S. George Scholarship fund. Additional observations were made on material collected near Burlington, Vermont, in the springs of 1955 and 1956 and these substantiate the earlier findings. Professor Irving J. Cantrall greatly assisted me with the field work and laboratory studies, while I was at the George Reserve.

Leg movements are described in terms of muscle actions. Such statements are presumptions based on a knowledge of the muscles present and I believe that this procedure results in a more accurate description of leg movements. The leg muscles are identical to those of *Unionicola* (Mitchell, 1955).

The behavior and accompanying secondary sexual modifications involved in pairing and insemination may be briefly outlined to show the characteristics common to the family Pionidae and then the contrasting situations in two subfamilies will be described to show that a process similar in broad outline is accomplished in very dissimilar ways in each subfamily.

Pairing of pionids results in the male placing a spermatophore in the gonoduct of the female. The male carries the spermatophore between the tips of the third legs, and usually the tarsal claws are modified into peculiarly-shaped spermatophore-bearing structures. Modifications in the length and shape of the last segment of the third leg may be essential for the animal to reach his own gonopore where the spermatophore is produced. Viets (1914) suggested that some substance secreted by the female was a stimulus for spermatophore production, at least in the genus *Typhys*. This is not supported by the studies reported below although no entirely clear answer is given. The importance of this point lies in the fact that the male must be carrying a spermatophore at the time of pairing if insemination is to result.

Most water-mites grasp and clutch any other similarly sized animal they

meet. If they contact a food organism, mosquito larvae or microcrustaceans in the case of pionids, there is an unhesitating, aggressive grasping followed by feeding. If another mite is encountered, the grasping is weaker and may be prolonged. Finally, if one of the opposite sex is encountered, and the female is receptive, pairing behavior will progress until the partners are held to each other in such a position that the spermatophore in the male's third leg will lie exactly over the gonopore of the female. The fourth legs of the males are constructed to serve as automatic positioning devices. In the few cases of improperly placed males there was no attempt at all to change the position of the spermatophore so that it would lie over the gonopore of the female.

Thus, each species has the proportions of the male's third and fourth legs and the position of the gonopore in both sexes exactly correlated. The simple mechanics of mating would eliminate insemination of any but similarly proportioned species and this may be the main barrier to interbreeding, which explains why there can be a lack of discrimination in the male's attempts at pairing.

#### GENUS PIONA

All members of the subfamily Pioninae have the fourth segment of leg four very greatly expanded and there is a deep rounded notch on its dorsal surface (fig. 3). Modifications in the chaetotaxy and shape of segments 5 and 6 are somewhat less prominent but they are among the characters used to distinguish species. Usually the terminal segment and tarsal claws of leg three are greatly modified spermatophore carriers and their structure is often of especial value for differentiating species.

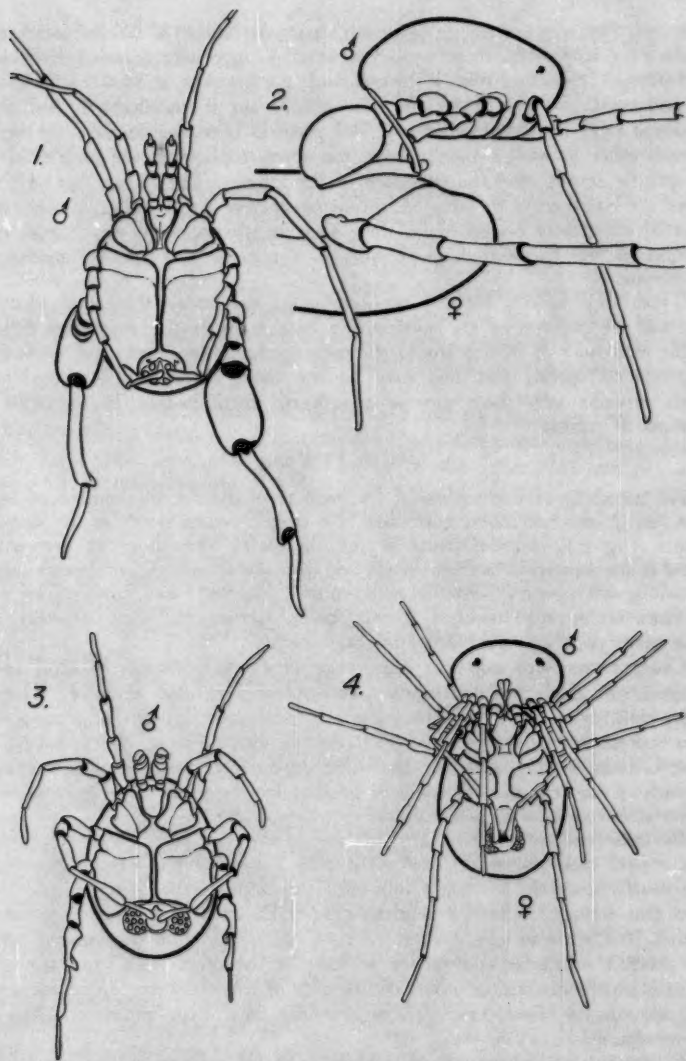
Observations were made on the mating of *Piona constricta* Wolcott and *P. clavicornis* Koch and both species were identical in their behavior. These observations agree with the details given in published accounts of mating in other species of *Piona* (Koenike, 1891; Piersig, 1900; Motas, 1928; Marshall, 1929; Uchida, 1932). The one detail that differs from one species to another is which of the legs of the female is grasped by the male. The species that I have observed show some individual variation in this trait.

*Piona* is continually active in nature and in the laboratory. When crawling over objects their movements are rapid and undirected but when swimming they usually move in a straight line until they strike some object. Any two mites that contact each other tend to grasp each other and crawl about one another. Male *Piona* will attempt to hold on to any mite encountered and will proceed with mating behavior as long as the other mite can be held. There is no discrimination shown on the part of the males nor do encounters with appropriate females seem to be anything other than undirected chance occurrences.

If insemination is to occur the male must be holding a spermatophore before the female is encountered. The spermatophore, held between the tips of the third legs, is normally held just over his gonopore (fig. 3). Males without spermatophores are accepted by females and will complete pairing behavior with no observable difference in the behavior of such pairs.

Receptive females of the proper species make less violent movements, whereas unreceptive females and mites of other species make movements so





Figs. 1-4.—1. *Tiphys brevipes* Habeeb male shown from the ventral aspect with the third legs in a position to pick up and carry a spermatophore. 2. Pairing position of *T. brevipes* Habeeb showing the lateral aspect of the two mites. Only the posterior portion of the female's body is shown. 3. *Piona constricta* Wolcott male shown from the ventral aspect with the third legs in a position to pick up and carry a spermatophore. 4. Pairing position of *P. constricta* Wolcott showing the ventral aspect of the female and the dorsal aspect of the male. The spermatophore is shown between the third legs of the male.

Note that the details of chaetotaxy have not been indicated in any of the figures.

violent as to free themselves from the males. When grasping a female of the proper species the male usually exhibits violent twitchings of leg four that apparently result from simultaneous contraction of all the segmental flexors of the leg. This is the only element of behavior that indicates recognition of the female by the male, and this reaction is not essential in eliciting mating behavior, nor is it necessary in the eventual accomplishment of insemination.

By the time ten seconds have elapsed the female is usually quiescent and lies with all legs fully extended. Usually by the end of a minute the male assumes a position with his venter on the anterior of the female (fig. 4). Segments of leg four are now tightly flexed, bending the leg into a full circle so that the segments bend back on themselves; thus the notch on the meso-dorsal surface is brought completely around and now faces meso-ventral relative to the male's body. In grasping the female these legs are pressed mesally so that the notch of segment four will engage the basal segment of leg two or three of the female and the male holds himself in position by pressing his fourth legs mesally, and the first two pairs of legs are no longer used to hold on to the female.

Observation of the male as he approaches the proper pairing position indicates this to be the result of random movements that persist until certain contact stimuli are obtained. The shape and contour of the female body is probably such that there is only one position in which proper contact is possible. The rare occasions when the male assumed an improper position were under crowded laboratory conditions, and these males were never as quiescent as were properly positioned males.

Generally the pair remains inactive throughout mating but if disturbance should bring about any activity of the pair it is always the male that makes swimming movements while the female remains inactive. When the pairing position is attained legs one and two of the male are extended mesoventrally, and the tip of leg three, which bears the spermatophore, rests directly over the female gonopore. Placement of the spermatophore is evidently automatic for incorrectly placed males make no adjustment in the position of the spermatophore relative to their body, and therefore cannot inseminate the female. After the position is attained there are slight contractions of the flexors of leg three that cause the tips of the legs to move back and forth, and, in normally positioned males, this means that the spermatophore is moved over the gonopore.

Females respond to this by contractions of the muscles inserting on the posterior genital stirrup which pulls the posterior part of the female gonopore inward, thus the anterior end projects relative to the posterior end, and, as the spermatophore is pulled anterior by the male, it tends to be pulled into the anterior part of the female gonopore. This accomplishes insemination and the pair usually separates within five minutes. It is not clear whether all, or only part, of the spermatophore is taken by the female.

Since the accomplishment of insemination requires the male to be bearing a spermatophore before pairing commences it is a matter of some importance to know what stimulates males to produce and carry a spermatophore. While precise answers are not given below it is clear that a combination of mechanical stimuli and some touch chemoreception are probably the main factors.

In the laboratory any male that is crowded by other mites may be bearing a spermatophore. Isolated males were never seen bearing a spermatophore even if they were placed in water or a container that had been occupied by a female. These observations indicate that sometimes mechanical contact alone may stimulate the males but that there does not seem to be any general chemical stimulant released into the water by the female. Even the slightest brush of a male with some part of the female will result in the male producing and picking up a spermatophore in his third legs. This male and female contact cannot be more than a brush for, if the male is able to grasp the female firmly mating will follow. Since crowding in nature is never so great as was the case in the laboratory it appears that spermatophore production in nature is generally the result of brushes between males and females.

#### GENUS TIPHYS

The terminal segments of leg three in the male are greatly modified in order to reach the gonopore and hold the spermatophore as is common throughout the family. Leg four has segments 4 to 6 greatly modified; segment four is expanded to an almost spherical shape and bears many long, fine setae; the two succeeding segments, though less modified in size, are usually peculiarly bent (fig. 1). Chaetotaxy and general form of the segments are characters of very great use in differentiating species and they have important biological functions in limiting interbreeding.

The behavior described below is based on observations of *Tiphys brevipes* Koch and *T. marshalli* Cook. *T. ornatus* Koch, which is very close to *T. brevipes*, and a related genus, *Pionopsis lutescens* Hermann, were studied by Viets (1914).

*Tiphys* shows the common response of grasping and crawling over any mite that is encountered. But this response is completely suppressed in receptive females and greatly modified in any males that encounter such females. Females that are ready to mate are inactive and rest on surfaces with the legs fully extended. Males are active at this time and many carry spermatophores with the tips of legs three (fig. 1). Most males will go through the motions of mating and females will accept them, but only those bearing spermatophores prior to pairing can inseminate the females.

Discovery of a female seems to be a chance encounter, although there must be prompt recognition to account for the immediate response by the male. The male ceases activity and may rest near the extended tips of the female's legs, or else will move very gently around the female just barely touching the tips of her legs. At this time the fourth legs of the male flex violently, and this leg action may throw the male a short distance away, occasionally he is thrown so far as to lose contact with the female.

This action persists and the female finally pounces on the male and holds him in a basket formed of her flexed legs. The male moves slightly while confined within the female's legs, but he is soon pressed to the venter of the female by the flexion of her legs. This takes one or two seconds and ends up with the male stuck to the venter of the female (fig. 2). The exact position of the male is determined by the curve of the fifth segment of leg

four which is what is held to the venter of the female. Just as soon as the male is firmly attached the female swims off while the male remains immobile throughout the rest of the pairing.

Some adhesive must be present to hold the male to the female but this was not observed nor is its source known. Females were seen to pass the third and fourth legs over the venter, whereas males were not observed to make any peculiar movements of leg four. This suggests that the female may secrete the adhesive. It is important that the male be precisely positioned and held there since the spermatophore must lie just over the female gonopore, and my observations indicate that the position of the spermatophore is in a fixed relationship to the male's body.

The pair is unusually active. When disturbed the female will swim off with the motionless male attached to her venter. The members of the pair are so closely appressed that the placement of the spermatophore cannot be observed. Within a short while, usually, the pair breaks up.

Experiments similar to those reported on *Piona* were carried out with *Tiphys marshalli* with similar results. Mechanical stimulation alone may cause the male to produce and carry spermatophores but brief contact with a female is the only completely effective stimulus. No response was obtained when the male was exposed to water in which the female had been kept.

#### DISCUSSION

Numerous workers have established the fact that the two subfamilies differ in many of the details of mating behavior but, in general, exhibit certain broad similarities in the mating process. All members of the family use the tarsal claw of the third leg as a spermatophore-bearer and all pionid males must be attached to the female in such a way as to automatically place the spermatophore over the female's gonopore. Since these features are common to all members of the family it is likely that they indicate mating habits that might well have been shared by an ancestral form. Possibly the fact that in both the Tiphysinae and Pioninae the venters of the pair are against each other and the male's anterior faces in a direction opposite from the female's can be considered as evidence of the mating position of the ancestral form.

These arguments are, of course, predicated on the well-supported view that the family is monophyletic. The main support for this conclusion is based on anatomy, and behavioral data can now be seen to offer some support for the view. Possibly a much more important contribution can be made toward understanding the subfamilies when the differences in the detailed behavior of the subfamilies are considered. It is shown that very significant differences define two phyletic lines and therefore verify a taxonomy that, until now, has been based on structure alone.

In the Pioninae aggressiveness of the male marks pairing, and any subsequent activity of the pair is due to the male. Positioning is accomplished by the locking of the fourth legs around the base of a pair of the female's legs.

The Tiphysinae are almost direct opposites in these traits. The male is relatively inactive in pairing while the female grasps and positions the male. There is the possibility that an adhesive that holds the male to the female

is produced by the female. This adhesive attaches segment four of leg four of the male to the fourth coxa of the female.

These contrasting behavioral differences add greatly to the significance that may be attached to the secondary structural differences between the subfamilies for they show that these correlate with remarkable behavioral differences involving both sexes. Thus, the combined evidence from both structure and behavior leaves little doubt that these are independently evolved phyletic lines that probably came from structurally similar ancestral forms that may well have had certain behavioral traits in common.

#### REFERENCES

- KOENIKE, F. 1891—Seltsame Begattung unter der Hydrachniden. Zool. Anz. 14:253-256.
- MARSHALL, RUTH 1929—The morphology and developmental stages of a new species of *Piona*. Trans. Wisc. Acad. Sci., A., and Lett. 24:401-404.
- MITCHELL, R. D. 1955—Anatomy, life history and evolution of the mites parasitizing fresh-water mussels. Misc. Pub. Mus. Zool. Univ. Mich. No. 89.
- MOTAS, C. 1928—Contribution à la connaissance des Hydracariens français particulièrement du Sud-Est de la France. Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble 20:1-373.
- PIERSIG, R. 1897-1900—Deutschlands Hydrachniden. Zoologica 22(1-6):1-601.
- UCHIDA, T. 1932—Some ecological observations on water-mites. J. Faculty Sci., Hokkaido Imp. Univ., Ser. VI. Zool. 1:143-165.
- 1940—Über den Begattungsakt bei *Forelia variegator*. Annot. Zool. Japonensis 19:280-282.
- VIETS, KARL 1914—Über die Begattungsvorgänge bei *Acercus*-arten. Inter. Rev. Hydrobiol. Hydrograph., Biol. Suppl. 6:1-10.



## A New Estheriid Conchostracan with a Review of the Other North American Forms

N. T. Mattox

University of Southern California, Los Angeles

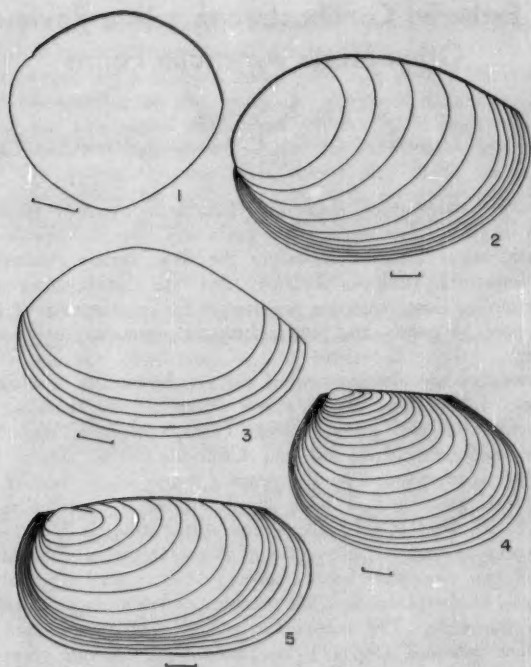
The order Conchostraca (subclass Branchiopoda) was established by G. O. Sars in 1867. The terms Phyllopoda and Eubranchiopoda have been used to designate a Division including the three orders Anostraca (fairy shrimp), Notostraca (tadpole shrimp), and the Conchostraca (the clam or claw shrimp). Conchostracans are frequently encountered in temporary, fresh water pools or ponds, and just as frequently present problems in proper identification.

The history of the classification of the conchostracans is a devious and confusing one. In the order there are now recognized five families. However, only four families are known from North America, the Lynceidae, Limnadiidae, Leptestheriidae, and the Cyzicidae. The family Lynceidae, Stebbing 1902, is represented by the genus *Lynceus* O. F. Muller, 1785, an easily recognized group with a wide North American distribution. *Lynceus brachyurus* O. F. Muller, with the widest distribution, is found in Europe and Asia as well as scattered over most of North America. The subspherical, bivalved shell (the two valves form a sphere) with no lines of growth (fig. 1) is characteristic of the genus as is the presence of but a single pair of claspers or claws in the male. The truncated rostrum of the male and the two-segmented first antennae (fig. 11) are also unique for this group which is represented in North America by four species: *L. brachyurus* O. F. Muller, 1785, *L. gracilicornis* (Packard) 1871, *L. mucronatus* (Packard) 1875, and *L. brevifrons* (Packard) 1877.

Another family with distinctive characters is the Limnadiidae Baird, 1849, including the North American genera *Limnadia* Brongniart, 1820, and *Eulimnadia* Packard, 1883. The presence of a pyriform frontal organ on the dorsal surface of the head is diagnostic for the limnadiids (figs. 12, 13). The shell of the limnadiids is extremely variable and is characterized by the absence of or poorly developed umbo region (figs. 2, 3). The members of the genus *Eulimnadia* possess a conspicuous spine, at the base of the cercopods, on the ventral surface of the telson. This spine is absent in the genus *Limnadia*. The North American *Eulimnadia* have been reviewed by Mattox (1945a). *Limnadia lenticularis* (Linné) (= *L. americana* Morse) is the only representative of that genus in North America.

The remaining types referred to as the "estheriids" are those that present the problems confronting us at this time. These are the conchostracans most frequently encountered and are the largest in the order, some grow to 16 mm in shell length.

The name *Estheria*, as a generic name for the group, was first applied by Ruppell in 1837. This name was incorrectly used for many years, since seven years earlier *Estheria* had been established for a genus of parasitic Diptera by Robineau-Desvoidy (1830). The name is currently used for this



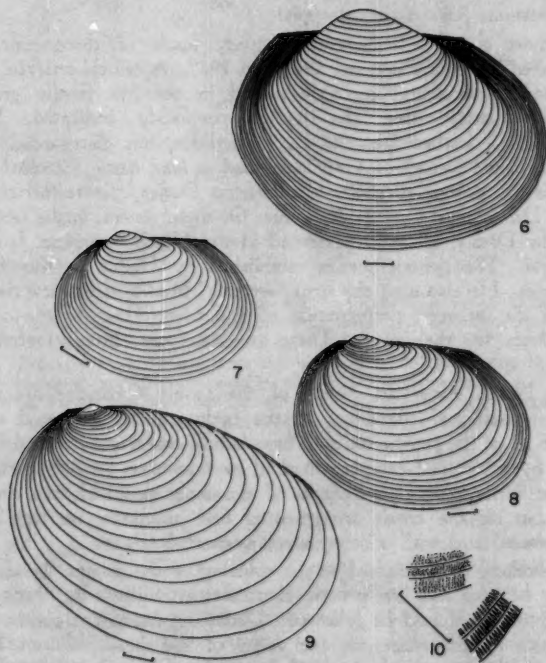
Figs. 1-5.—1. *Lynceus brachyurus*, shell, from Illinois; 2. Shell of *Limnadia lenticularis*, from Woods Hole, Massachusetts; 3. Shell of *Eulimnadia inflecta*, from Illinois; 4. Shell of *Caenestherella setosa*, from Texas; 5. Shell of *Leptestheria compleximanus*, from Texas. All scales equal 1.0 mm.

group of flies and no synonym is available for the genus. Actually the first "estheriid" was placed in the genus *Limnadia* by Krynicki (1830). It was Audouin in 1837 who used the first valid name for the group when he removed *Limnadia tetracera* to the new generic designation *Cyzicus*, and gave diagnostic differences between *Cyzicus* and *Limnadia*. This action thus made *Cyzicus tetracera* (Krynicki) the type species by monotypy. This conforms with the Law of Priority, Article 25 of the "Regles," since a particular species "designation" was given. Unfortunately the designation by Audouin was disregarded with the synonym *Estheria* being perpetuated. However, as here indicated, *Estheria* Ruppell as applying to these crustaceans must be ruled out on the basis of the Law of Priority, as well as homonymy. Keilhack (1909, 1910) was apparently the first worker to publish the indication of the homonymy of *Estheria* Ruppell, 1837, and *Estheria* Robineau-Desvoidy, 1830. Keilhack also made it clear that *Cyzicus* Audouin should be used for this group of crustacea.

To add to the confusion, M. N. Joly (1842) reviewed the group known

at that time and even though he recognized the prior designations of *Estheria* and *Cyzicus* he proposed a new generic name *Isaura* with the type species *cycladoides*. This name *Isaura* has been revived by paleontologists who insist it is a valid name (Bock, 1953). However, we must again disregard *Isaura* as a synonym, on the basis of the Law of Priority, in favor of *Cyzicus*. Likewise the family name Isauridae Bock must be rejected.

Sars (1888) made the first division from the perpetuated generic name *Estheria* when he described the genus *Cyclestheria*, and later (1900) created the family Cyclestheriidae for this genus. This is the only family of the order not represented in North America. In 1898 Sars made a further division when he described the genus *Leptestheria*. This genus is unique in possessing a spine on the anterior termination of the rostrum. *L. compleximanus* (Packard) 1877, the only North American representative of this group, was described by Packard first as a *Eulimnadia* and later placed in the genus *Estheria*. Figs. 14a and 14b represent the lateral aspects of the head of the



Figs. 6-10.—6. Shell of *Cyzicus morsei*, from Oklahoma; 7. Shell of *Caenestheriella belfragei*, from Oklahoma; 8. Shell of *Cyzicus mexicanus*, from Illinois; 9. Shell of *Cyzicus californicus*, from San Francisco, California; 10. Two areas of different shell sculpture on same shell of *Cyzicus mexicanus*, from Texas. Scale for fig. 10 is equal to 0.5 mm, all others are 1.0 mm.

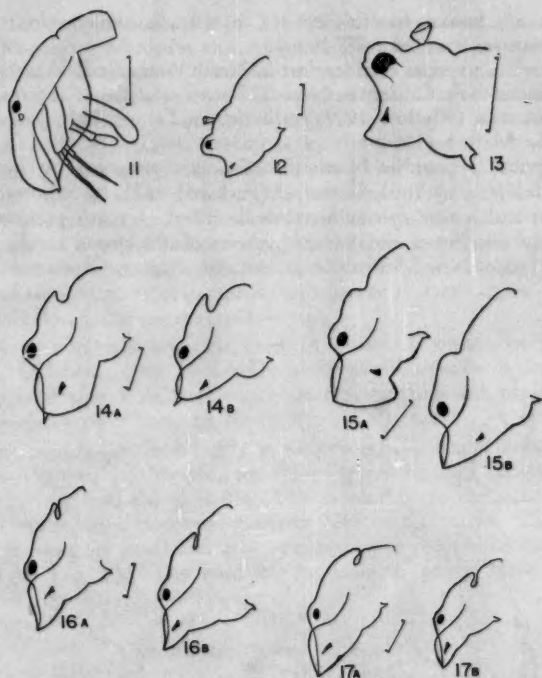
two sexes of this species, and fig. 5 illustrates the characteristic elongated, subrectangular and compressed shell of *L. compleximanus*. Daday (1915) created the family Leptestheriidae to include this and two other genera, all with the terminal rostral spine.

The family designations for the various estheriids have also varied. Baird first placed all conchostracans in one family. Packard (1883) used the same name, Limnadiidae, with the subfamily Estherianae in accord with his incorrect use of the generic name *Estheria* to designate all estheriids. It was Stebbing (1910) who established a family for the estheriids, other than the Cyclestheriidae and Leptestheriidae, when he designated the Cyzicidae with *Cyzicus* as the proper type genus. Based on Decision 54 of the XIV International Congress of Zoological Nomenclature at Copenhagen, 1953, there seems to be no question as to the validity of this family name. This decision indicated that the family name changes when the original type genus is shown to be a junior homonym and that the family name would then be taken from the oldest available generic name, in this case *Cyzicus*. The old name Estheriidae Sars is thus dropped.

The most complete monographic study made of these conchostracans was published by Daday between 1915 and 1927. A critical analysis was made of all known forms and correctly placed in the five family groups now recognized. Daday used the names previously indicated, Lynceidae, Limnadiidae, Cyclestheriidae, and Leptestheriidae, but disregarded the name of Stebbing and instead of Cyzicidae used a new name Caenestheriidae to incorporate the generic divisions *Caenestheria* Daday, *Caenestheriella* Daday, *Eocyclus* Daday, and *Cyzicus* Audouin. Of these genera, in the latter family, proposed by Daday, all are represented in the North American fauna except *Caenestheria*. The generic names established by Daday in this family are all valid ones. He also used the stem "estheria" in two of his new designations because of the incorrect perpetuation of and in reference to the old generic name *Estheria* for the group. These are the forms usually referred to as "estheriids."

If the North American genera of the family Cyzicidae are examined, definite morphological characters of the body can be indicated which are common to all of the generic units. These family characters are: conchostracans enveloped by a bivalved carapace marked by numerous growth lines; the first and second post-cephalic appendages of the male modified into claspers; no frontal organ on the head; unsegmented first antennae; no terminal spine on the rostrum; and with a conspicuous truncated telson.

Some workers have objected to the splitting of the original genus *Cyzicus*. The writer believes that the generic characters established by Daday (1915) are significant and should be followed. Daday separated the genera primarily on the basis of differences in the form of the head. *Caenestheriella* is characterized by possessing an extended, compressed, and acutely terminating rostrum in both sexes, and with a conspicuous and deeply cleft occipital notch (figs. 16 and 17). In *Eocyclus* the rostrum of the female terminates acutely, but in the male the rostrum is spatuliform in lateral profile view. The occipital notch is shallow and rounded (fig. 15). Members of the genus *Cyzicus* have the same sexual dimorphism in the form of the rostrum as in



Figs. 11-17.—11. Head of male *Lynceus brachyurus*, from Illinois; 12. Head of female *Limmadia lenticularis*, Massachusetts; 13. Head of male *Eulimnadia inflecta*, from Illinois; 14. *Leptesteria compleximanus*, a. male and b. female head, from Texas; 15. Heads of *Eocyclus concavus*, a. male and b. female, from Texas; 16. Heads of *Caenestheriella setosa*, a. male and b. female, from Texas; 17. Heads of *Caenestheriella belfragei*, a. male and b. female, from Oklahoma. Scales all equal 1.0 mm.

*Eocyclus*, but the occipital notch is deeply cleft and terminates acutely (figs. 18-20).

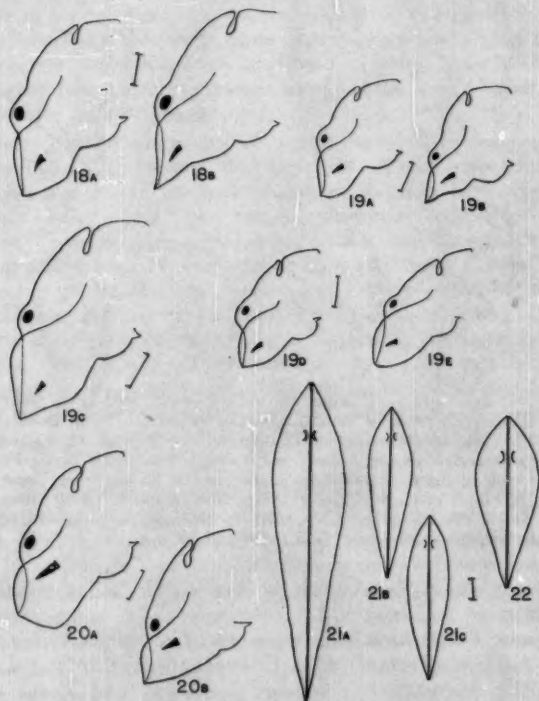
The genus *Caenestheriella* is represented in North America by three species; *C. belfragei* (Packard) 1871, *C. setosa* (Pearse) 1913, and *C. gynecia* Mattox, 1950. *Caenestheriella belfragei* is known from Texas, Oklahoma, and Kansas. This species is characterized by a thick, globose shell, 21 to 35 growth lines, with a prominent umbo (fig. 7), and an average of 7.5 mm in shell length by 6 mm in width or height. The second antennae have 14 or 15 segments in the flagella, as is characteristic of the genus. *Caenestheriella setosa* has been collected in Nebraska, Oklahoma, Kansas, South Dakota, Oregon, Texas, and Missouri. The shell is more elongate than *C. belfragei*. less conspicuous umbo (fig. 4), an average of 15 lines of growth, and a telson with 10 to 15 spines. *Caenestheriella gynecia* is known only from Ohio.



No males are known for this species, a character unique for the North American species (see Mattox, 1950).

There are two species of *Eocyclus* in North America; *E. digueti* (Richard, 1895) recorded from California, Nevada, Kansas, and Baja California, Mexico, and *E. concavus* (Mackin, 1939) collected in Texas. This genus has been reviewed by Mattox (1954b).

The genus *Cyzicus* in North America is represented by four species; *C. mexicanus* (Claus) 1860, *C. morsei* (Packard) 1871, *C. californicus* (Packard) 1874, and a new species herewith described. *Cyzicus mexicanus* is the most widely distributed and variable species of the genus having been collected in Mexico, New Mexico, Texas, Arizona, Kansas, Oklahoma, Nebraska,



Figs. 18-22.—18. Heads of *Cyzicus morsei*, a, male and b, female, from Oklahoma; 19. Heads of *Cyzicus mexicanus*, a, male and b, female from Virginia, c, male from Illinois, d, male from New Mexico, and e, male from Texas; 20. Profile views of heads of *Cyzicus californicus*, a, male and b, female from San Francisco, California; 21. Dorsal views of the shell of *Cyzicus californicus*, a, Pacific Grove, b, Goleta, and c, Oakland, California; 22. Dorsal view of shell of *Cyzicus elongatus*, from Los Angeles, California. All scales equal 1.0 mm.

Arkansas, Illinois, Tennessee, Ohio, Kentucky, Pennsylvania, West Virginia, Virginia, Maryland, Manitoba and Alberta. The shell of *C. mexicanus* (fig. 8) is moderately swollen with conspicuous umbones approximately one-fourth the length from the anterior end. The general form and color of the shell is somewhat variable as is the profile appearance of the head of the male (fig. 19 a, c, d, e). These variations in the form of the male rostrum range from an extremely truncated form to a broadly rounded profile development. In all cases, however, the rostrum is much more broad than the acutely pointed rostrum of the female. The surface sculpture of the shell also varies from a granulated to ridged appearance as seen in fig. 10 which illustrates two areas on the same shell. This shell sculpture has been used by different workers to separate species and genera in fossil forms; a category which obviously should not be used.

*Cyzicus morsei* has been collected in North Dakota, South Dakota, Nebraska, Oklahoma, and Iowa. The shell of this species is distinctive, it is very globose with a nearly centrally located umbone and possesses many closely crowded growth lines, fig. 6.

*Cyzicus californicus*, found only in California, also has a distinctive shell. The shell is greatly compressed, the thickness of the shell is approximately 20% of the length of the shell (fig. 21) in contrast to the swollen shell of *C. morsei* which has a thickness of nearly 50% of the length. The umbones of *C. californicus* are small and arise at the anterior end of the curved dorsal shell margin (fig. 9). The head of the male in profile view is strongly spatuliform (fig. 20a).

#### *Cyzicus elongatus* sp. nov.

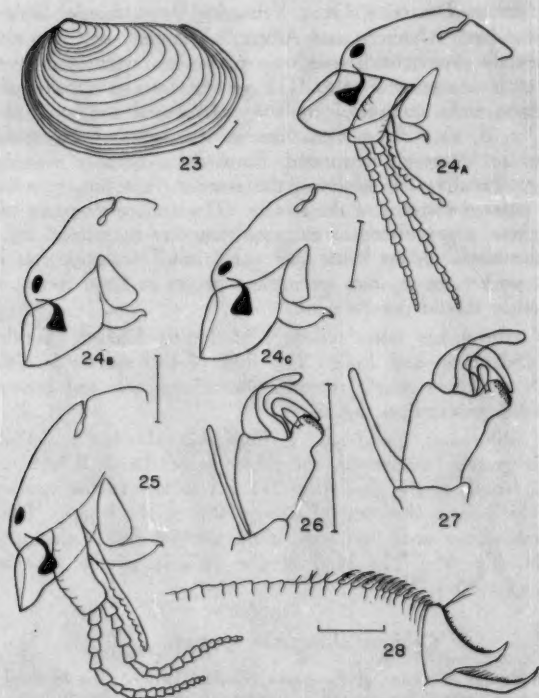
*Male*.—With the characters of the genus (Daday, 1915). The bivalved shell (fig. 23) is elongate in general outline and is compressed laterally, the thickness is approximately one-third that of the length of the shell (fig. 22). The greatest height of the shell is approximately 60% of the length; an average shell size is 7.3 mm in length by 4.3 mm in width and 2.4 mm thick (from side to side). The umbo is not conspicuous and is located approximately one-fifth the length of the shell from the anterior end. The adult shell possesses an average of 18 concentric lines of growth. In life the color of the shell varies from a transparent amber to a dark brown.

The head (fig. 24a, b, c) is broadly triangular in profile view. The rostrum is variable, widely truncate to a broadly pointed rostrum. The occipital angle is projected forming a deep, narrow cervical groove. The second antennae possess two rami, normally 16 segments each. The first antennae extend to approximately the seventh segment of the second antennae. The medianly located ocellus is large and very conspicuous.

The trunk consists of 23 segments, each bearing a pair of appendages. The posterior twelve segments bear prominent dorsal papillae, each laterally spined (fig. 28). The telson is narrowly truncated dorsally, greatly extended ventrally and bears an average of 31 dorso-lateral spines. The cercopods are strongly curved and extend beyond the ventral spines of the telson.

The paired trunk appendages are all typical foliaceous phyllopod "legs" except for the first two pairs of claspers. These two appendages are similar in form except that the digitiform sixth endite of the second pair is longer than that of the first pair (figs. 26, 27). The thumblike extension of the fourth endite of the first pair has a moderately depressed notch at the base.

*Female*.—The female shell is very similar in form to that of the male. The head of the female is more narrowly elongate than that of the male and in profile is seen to be acutely pointed, not truncate as in the male (fig. 25). The first antennae are shorter than



Figs. 23-28.—*Cyzicus elongatus*. 23. Shell of male; 24a, b, c. Variations in profile of male head; 25. Profile of female head; 26. First clasper of male; 27. Second clasper of male; 28. Dorsal edge of trunk segments and the telson. All scales equal 1.0 mm.

in the male, they extend only to the fourth segment of the rami of the second antennae. The occipital notch is deeply cleft. The trunk appendages are all typical except numbers 9 and 10 which have elongate epipodites modified for bearing the egg masses.

*Type locality*.—Temporary pool in Los Angeles Co., California.

*Types*.—Holotype, male, USNM No. 99524; paratypes, both sexes, USNM No. 99525, and in the writer's collection.

Specimens of *Cyzicus elongatus* were first collected in a temporary fresh-water pool in Los Angeles County on April 7, 1954. This pool did not fill during the spring of 1955, but in April 1956 these animals were again present in the same pool. In all collections the females were only slightly more abundant. In the original collection there were 30 females and 28 males. Specimens have also been taken in other areas in southern California. *Cyzicus elongatus* seems to be closely related to *C. californicus*; there are, however, several differences between the two species. The shell of *C. elongatus* is more elongate than that of *C. californicus*; the dorsal shell margin is straight

in *C. elongatus* and markedly curved in *C. californicus*; the shell height of *C. elongatus* is approximately 60% that of the length and in *C. californicus* it is 70% of the length; the width of the shell through the thickest part of the body in *C. elongatus* is approximately one-third the length of the shell and in *C. californicus* the thickness is one-fourth the shell length (figs. 21 and 22). The form of the head of the male of *C. elongatus* is variable and more nearly like that of *C. mexicanus* and does not approach that of the broadly truncated rostrum of *C. californicus*. The antennae are similar to those of *C. mexicanus*, not as long as those of *C. californicus*. The dorsal trunk spination of *C. elongatus* is confined to the posterior 12 body segments, in *C. mexicanus* the posterior 14, and in *C. californicus* the posterior 16 to 18 segments. The telson of *C. elongatus* is not as broad as that of either *C. mexicanus* or *C. californicus*. The male claspers of *C. elongatus* are more narrow than those of the other species and the terminal endites are shorter. The other North American species of the genus, *C. morsei*, with a heavy, globose shell and with body features more robust and heavier cannot easily be confused with *C. elongatus*. The concentric lines on the shell seem to be true "growth lines" of the sort as seen on the shell of pelecypod mollusks. These growth lines are apparently added in the same fashion as in clams and are not involved with ecdysis except to mark such interruptions of growth. The body covering is lost during ecdysis, but not the shell. The number of growth lines seems to be the result of variable environmental conditions. These conclusions are based on extended observations of living animals of several species which were maintained in the laboratory.

By comparing the shell characters of these species it is seen that details of shell form and sculpture are extremely variable within a genus, and in some cases species. For example, the shells of *Cyzicus morsei*, *C. mexicanus*, *C. californicus*, and *C. elongatus* are very different yet all are members of the same genus as determined by characters of the body morphology. It is also seen that the shell of *Cyzicus morsei* is very similar to that of *Caenestheriella belfragei* and the shell of *Cyzicus mexicanus* is very similar in form to that of *Caenestheriella setosa*. Paleontologists have discovered and named innumerable fossil conchostracans with many genera and species being named on the basis of minute differences of the shell such as granulations, ridges, and the shape of the shell, characters which have no consistent value for separating the various taxa, especially above the species level. Workers, such as Raymond (1946) and Bock (1953), state the inadvisability of using shell characters alone to separate genera, yet in the same papers use shell characters in the absence of other features to establish new genera. In the writer's opinion all of the fossil estheriids, except those with a prominent lateral carina on the shell which are members of the genus *Leaia* Jones, 1862, should be placed in the one genus *Palestheria* Barnard, 1929. Certainly there is no constant set of characters that can be used consistently to separate the numerous genera that have been proposed by paleontologists.

This stand is taken in view of the lack of knowledge of the animal characters in practically all cases. A marked exception to this is that reported by Wright (1920) where numerous appendages of an estheriid were found fossilized. That species, *Limnetheria ardra* Wright, was placed with

the lynceids (*Lynceus* = *Limnetis*) on the basis of the interpretation that these animals possessed but a single pair of claspers. In the writer's opinion this interpretation is entirely erroneous. These animals seem to have definitely had the first two pairs of appendages modified into claws as in the living estheriids. Plate XXIV, figs. 1 and 1b in Wright's paper show clearly two different claws with the same differences in form as in living species. The second pair has a longer claw and also a longer and differently shaped terminal segment. These two claspers undoubtedly came from the same side of the body, not one from each of the two body sides as suggested by Wright; there is only one mandible shown in this same figure which further supports the idea of the appendages preserved as representing those from one side of the body only. The well preserved antennae and telson are very similar to those of modern estheriids indicating the close relationship of those Carboniferous forms with living species. Family designations of fossil species can not be made definite because of the lack of knowledge of the body morphology of most of the ancient forms. However, in view of what is known about most of the fossil estheriids it is not unreasonable to place them in the family Cyzicidae with the living species of that group.

From this general review it can be seen that a great deal of comparative study of living and fossil forms must be completed before these questions of relationships can be answered satisfactorily. It is hoped that such a study will be possible in the near future.

#### REFERENCES

- AUDOUIN, VICTOR 1837—Seance du 1 fevrier 1837. Ann. Soc. Entomol. France. 6:9-11.
- BAIRD, W. 1849—Monograph of the family Limnadiidae, a family of entomostracous crustacea. Proc. Zool. Soc. London. Pt. 17:84-90.
- BARNARD, K. H. 1929—Contributions to the crustacean fauna of South Africa. No. 10. Revision of the Branchiopoda. Ann. So. Afr. Mus. 29(1):181-272.
- BOCK, W. 1953—American Triassic estherids. J. Paleont. 27(1):62-76.
- DADAY, E. 1915—Monographie systematique des phyllopoques conchostraces. Ann. Sc. Nat. Zool. 20, Ser. 9:39-330.
- 1923—*Ibid.* 6, Ser. 10:255-390.
- 1925—*Ibid.* 8, Ser. 10:143-184.
- 1926—*Ibid.* 9, Ser. 10:1-81.
- 1927—*Ibid.* 10, Ser. 10:1-112.
- JOLY, M. N. 1842—Recherches zoologiques, anatomiques et physiologiques sur l'*Isaura cycladoides*, nouveau genre de Crustace à test bivalve, decouvert aux environs de Toulouse. Ann. Sc. Nat. Zool. 17, Ser. 2:293-349.
- KEILHACK, L. 1909—Die Süßwasserfauna Deutschlands, Heft 10: Phyllopoda.
- 1910—Zur Nomenklatur der deutschen Phyllopoden. Zool. Annal. Zeit. Gesch. Zool. 3:177-184.
- KRYNICKI, JEAN 1830—Des Limnadies. Bull. Soc. Imper. Natur. Moscou. No. 2:173-182.
- MATTOX, N. T. 1950—Notes on the life history and description of a new species of conchostracan phyllopod, *Caenestheriella gynecia*. Trans. Amer. Micro. Soc. 49(1):50-53.
- 1954a—A new *Eulimnadia* from the rice fields of Arkansas with a key to the American species of the genus. Tulane Stud. Zool. 2(1):3-10.



- 1954b—Description of *Eocyclus concavus* (Mackin) with a review of other North American species of the genus (Crustacea: Conchostraca). J. Wash. Acad. Sci. 44(2):46-49.
- PACKARD, A. S. 1883—A monograph on the phyllopod Crustacea of North America. 12th Ann. Rept. U. S. Geol. and Geogr. Surv. Terr., 1878 (Hayden Survey), Part I:295-592.
- RAYMOND, P. E. 1946—The genera of fossil conchostraca—an order of bivalved crustacea. Bull. Mus. Comp. Zool. 93(3):217-307.
- ROBINEAU-DESVOIDY, J. B. 1830—Essai sur les Myodaires. Mem. Acad. Sc. de Inst. France, Sc. Math. et Phys. T. 2:305.
- RUPPEL, E. in STRAUS-DURCHHEIM, H. 1837—Ueber *Estheria dabalacensis*, Ruppel neue Gattung aus der Familia der Daphniden. Abh. Senckenbg. Mus. 2(2):117-128.
- SARS, G. O. 1867—Histoire naturelle des Crustacés d'eau douce de Norvege. Premiere livraison. Les Malacostraces. Christiania 1867.
- 1888—On *Cyclestheria hislopi* (Baird), a new generic type of bivalve Phyllopoda. Norske Viden. Selsk. Forh. aar 1887 (1):1-65.
- 1898—Description of two additional South-African Phyllopoda. Arch. Math. Naturvidenskab 20(6):9.
- 1900—On some Indian Phyllopoda. *Ibid.* 22(6).
- STEBBING, THOMAS R. R. 1910—General Catalogue of South African Crustacea. Ann. So. Afr. Mus. 6(4):281-599.
- WRIGHT, M. C. 1920—*Limnetheria*: a new conchostracan genus from the Kilkenny Coal-measures. Proc. Roy. Irish Acad. 35(10):187-204.

## Parasitic Copepoda from Louisiana Fresh Water Fish

David Causey

University of Arkansas, Fayetteville

No truly monographic survey of the parasitic Copepoda of American freshwater fish has been made. Wilson, in his numerous papers surveying taxonomic groups, necessarily included freshwater species. In two papers (Wilson, 1914 and 1917) he dealt with freshwater forms exclusively. Numerous papers and bulletins on the parasites of freshwater fish mention copepods, usually rather incidentally. *Argulus* sp. and *Ergasilus caeruleus* appear to be the most widespread species in such literature.

The present report is based upon material from Louisiana freshwater fish collected during 1955 and kindly sent to me by Dr. Harry J. Bennett of Louisiana State University. There were 49 collections in which parasitic copepods had been observed. In a few cases the actual parasites had been separated in vials while in the rest the collections were either pieces of flesh from which lernaids hung, or gills upon which there were ergasilids. I failed to find parasites in five samples, neither on the gills nor in the slime and detritus in the bottom of the containers. These probably had ergasilids on them which had become lost or were overlooked. They were from fish well represented by other specimens in this survey. It is my understanding that this material came from the fish recognized to be parasitized with copepods. I have no information which would allow any speculation as to the possible incidence of infection. Five years of experience with Gulf of Mexico copepod parasites lead me to think, considering the difficulties of fair sampling, age factors, life history factors, etc., that statements of incidence of infection for copepods have little value.

Four genera and 12 species are represented in the collection. Of these, *Argulus* is the textbook parasitic copepod, readily recognized by its flat, scale-like body and the two ventral suckers. It occurs on the body surface of the fish, where it moves about readily. It has a tendency to let go as the fish is lifted from the water, so that many specimens are lost in this way. It is sometimes found swimming freely in the water. The female leaves the host fish to lay her eggs on some submerged object. Because of this habit it lacks the two egg sacs so typical of copepods. *Lernaea* is also found on the surface, usually back of a fin, with its anchor-like anterior end deeply embedded in the host's flesh. *L. cyprinacea* (= *L. carassii* Tidd) is regularly referred to as the "anchor parasite" in texts on fisheries, but I think fishermen who have noticed them refer to the whole genus as "anchor worms." The members of the genus *Ergasilus* are minute gill parasites. Occasionally only a few are present, but they may be so numerous as to suggest that the gills have been peppered. A little magnification will show the second antennae, a pair of vicious appearing claws, clasping the gill filament, either at the very end of the filament or higher up. The last of the four genera, *Achtheres*, could be confused with *Salmincola* by a determined individual, but the absence of an

TABLE 1.—Checklist of parasitic copepoda of Louisiana freshwater fish

Parasite	Host	Locality and Notes
<b>ARGULOIDA</b>		
<b>ARGULIDAE</b>		
<i>Argulus flavescens</i> Wilson	<i>Micropterus punctulatus</i> , Kentucky Bass	Alabama Landing, Ouachita River, 1 collection
<i>A. mississippiensis</i> Wilson	<i>Lepisosteus osseus</i> , Longnose Gar	Ouachita River at Monroe, 1 collection
<b>CYCLOPOIDA</b>		
<b>ERGASILIDAE</b>		
<i>Ergasilus caeruleus</i> Wilson	<i>Pomoxis nigromaculatus</i> , Black Crappie	Ouachita River at Monroe, 1 collection
<i>E. elongatus</i> Wilson	<i>Micropterus dolomieu</i> , Northern Smallmouth bass	Aroudant Creek or James Pond, 1 collection
<i>E. mugilis</i> Vogt	<i>Polyodon spathula</i> , Spoon-bill Catfish	Cobell Bay, S.E. of Baton Rouge, 1 collection
<i>E. vernicolor</i> Wilson	<i>Mugil curema</i> , Mullet	Old River at Morgana, 1 collection
	<i>Chaenobrytus coronarius</i> , Warmouth Bass	Big Corney, 1 collection
	<i>Ictalurus furcatus</i> , Blue Catfish	Old River, 7 collections; Jonesville, 4 collections;
		Archafalaya River at Jonesville, 1 collection
	<i>Lepomis macrochirus</i> , Common Bluegill	Alabama Landing, Ouachita River, 1 collection
	<i>Lepisosteus spatula</i> , Mississippi Alligator Gar	Alabama Landing, Ouachita River, 2 collections
	<i>Micropterus punctulatus</i> , Kentucky Bass	Alabama Landing, Ouachita River, 7 collections
		Big Corney, 2 collections
	<i>Roccus chrysops</i> , White Bass	Ouachita River at Monroe, 1 collection
	<i>Morone interrupta</i> , Yellow Bass	Old River, 1 collection
	<i>Pylodictis olivaris</i> , Flathead Catfish	Alabama Landing, Ouachita River, 1 collection
<b>CALIGOIDA</b>		
<b>LERNAEIDAE</b>		
<i>Lernaea anomala</i>	<i>Micropterus punctulatus</i> , Kentucky Bass	Big Corney, 3 collections
<i>L. cruciata</i> (Le Sueur)	<i>M. salmoides</i> , Largemouth Bass	Lake Chicot, 1 collection
	<i>Ambloplites rupestris</i> , Northern Rock Bass	Vidrine Lake, near Ville Platte, 1 collection
	<i>Micropterus salmoides</i> , Largemouth Bass	Lake Chicot, 1 collection
	<i>M. dolomieu</i> , Northern Smallmouth Bass	Vidrine's Lake, near Ville Platte, 1 collection
<i>L. cyprinacea</i> Linnaeus	<i>Ictalurus punctatus</i> , Blue Catfish	Ouachita River, near Monroe, 1 collection
<i>L. tenuis</i> Wilson	<i>Aplocheilichthys grunniens</i> , Freshwater Sheepshead	Ouachita River, near Monroe, 1 collection
<b>LERNAEOPODOIDAE</b>		
<b>LERNAEOPODIDAE</b>		
<i>Achtheres lacae</i> Kröyer	<i>Ictalurus furcatus</i> , Blue Catfish	Old River; Lake Chicot, 5 collections
<i>A. micropteri</i>	<i>Micropterus salmoides</i> , Largemouth Bass	Lake Chicot, 3 collections

abdomen in *Salmincola* and its presence in *Achtheres* is a good offhand difference. Since *Salmincola* is associated with trout and salmon, it is unlikely that it will turn up in Louisiana fish. *Achtheres*, like some other genera of parasitic copepods, tempts one into anthropomorphism. The body is rather human-like, and the two arms clasping the bulla suggest a prayerful attitude far from the actual truth! These occur on the gills or the gill arches and are large enough to be seen easily with the naked eye.

With the exception of the textbook *Argulus*, which lives on mucus, all these copepods (including the real *Argulus*!) are blood sucking parasites. It is difficult to assess the damage done. Obviously the number of parasites pres-

TABLE 2.—Checklist of Louisiana host fish and their parasitic Copepoda

Fish	Copepod
<i>Ambloplites rupestris</i> , Northern Rock Bass	<i>Lernaea cruciata</i>
<i>A. grunniens</i> , Freshwater Sheepshead	<i>L. tenuis</i>
<i>Chaenobryttus coronarius</i> , Warmouth Bass	<i>Ergasilus versicolor</i>
<i>Ictalurus furcatus</i> , Blue Catfish	<i>Achtheres lacae</i>
	<i>Ergasilus versicolor</i>
	<i>Lernaea cyprinacea</i>
<i>Lepisosteus osseus</i> , Gar	<i>Argulus mississippiensis</i>
<i>L. spatula</i> , Mississippi Alligator Gar	<i>Ergasilus versicolor</i>
<i>Lepomis macrochirus</i> , Common Bluegill	<i>E. versicolor</i>
<i>Micropterus dolomieu</i> , Northern Smallmouth Bass	<i>E. caeruleus</i>
	<i>Lernaea cruciata</i>
<i>M. Punctulatus</i> , Kentucky Bass	<i>L. anomala</i>
	<i>Argulus flavescens</i>
	<i>Ergasilus versicolor</i>
	<i>Lernaea anomala</i>
<i>Micropterus salmoides</i> , Largemouth Bass	<i>Achtheres micropteri</i>
	<i>Lernaea anomala</i>
	<i>L. cruciata</i>
<i>Roccus chrysops</i> , White Bass	<i>Ergasilus versicolor</i>
<i>Morone interrupta</i> , Yellow Bass	<i>E. versicolor</i>
<i>Mugil curema</i> ,* Mullet	<i>E. mugilis</i>
<i>Pylodictis olivaris</i> , Flathead Catfish	<i>E. versicolor</i>
<i>Polydon spathula</i> , Spoon-billed Catfish	<i>E. elongatus</i>
<i>Pomoxis nigromaculatus</i> , Black Crappie	<i>E. caeruleus</i>

\* A marine fish. The record is not an error.

ent is an important factor. Probably a *lernaeid*, with its anterior end deeply embedded in the flesh (often causing a tumor-like mass), does the most damage per parasite. Whether the one, two, or three I have found present on a fish in these samples are worse than the *ergasilids*, running up to possibly several hundred, must be left as a matter of personal opinion. With fish in their natural waters copepods probably take only a minor toll. In fish hatcheries and fish ponds an entirely different set of environmental factors may apply, e.g., crowding, unnatural food, etc. Then any of these parasites may become a serious factor. This is well known for the *lernaeids*.

Data regarding the species, their hosts, and the localities from which they were obtained are presented in table 1. Keys to the genera and species are also provided. The key to the genera, using admittedly superficial characteristics, will allow the determination of the genera considered in this report. To determine the species requires the working out of details with considerable care, and, of course, access to the literature. The task is made more difficult, especially in *argulids* and *lernaeids*, by a lamentable lack of agreement among the specialists as to which species are valid, and what characteristics are pertinent. The keys included will allow a reasonable approximation of the species included in this report if used for mature females with well developed egg sacs. The best a key for most of the parasitic Copepoda can do is to narrow the probability to a limited number of possible species. Then the actual details must be established. If this is done first, one doesn't need a key!

#### KEY TO GENERA OF PARASITIC COPEPODA

- 1 (4) Gill parasites .....2
- 2 (3) Minute (2 mm or less in length) parasites with second antennae modified into a pair of long, three segmented clasping claws .....*Ergasilus*.
- 3 (2) Larger (4 mm or more in length) parasites with second maxillae modified into long arm-like structures whose ends are attached to a bulla embedded in the flesh of the host .....*Achtheres*
- 4 (1) Surface parasites .....5
- 5 (6) Scale-like; the second maxillae are modified into a pair of conspicuous suckers; moves over the surface of the host .....*Argulus*
- 6 (5) Thread or worm-like, with anterior end deeply buried in the flesh of the host and anchored by two, three, or four processes which roughly resemble an anchor; immovable .....*Lernaea*

#### KEYS TO SPECIES OF PARASITIC COPEPODA

##### Genus *Achtheres*

- 1 (2) Arms stout, not quite as long as body .....*A. micropteri*
- 2 (1) Arms more slender, as long as the body .....*A. laeae*

##### Genus *Argulus*

- 1 (2) Body small (to 6 mm in length); respiratory areas in carapace a large posterior one and a small anterior one along the carapace margin on either side; suckers have supporting ribs of four to six rods .....*A. flavescens*
- 2 (1) Body large (to 15 mm or more in length); respiratory areas in carapace a large posterior one and a small anterior one in a notch of the former; suckers have supporting ribs of three or four rods .....*A. mississippiensis*



Genus *Ergasilus*

- 1 (2) Cephalothorax definitely divided into head and first thoracic segment by a transverse furrow; egg sacs about twice the length of the body; unlikely in freshwater fish ..... *E. mugilis*
- 2 (1) Cephalothorax not so; egg sacs approximately the length of the body ..... 3
- 3 (6) Cephalothorax hourglass shaped (sides re-entrant) ..... 4
- 4 (5) Cephalothorax definitely hourglass shaped; egg sacs probably not as long as the body; proximal segments of second antennae not inflated or swollen; usually with epizoid or epiphytic organisms ..... *E. versicolor*
- 5 (4) Cephalothorax slightly hourglass shaped; egg sacs about the same length as the body; proximal segments of second antennae inflated or swollen; without epizoid or epiphytic organisms ..... *E. caeruleus*
- 6 (3) Cephalothorax not hourglass shaped but elliptical and with smooth sides; egg sacs about the same length as the body ..... *E. elongatus*

Genus *Lernaea* (adapted from Wilson)

- 1 (2) Two cephalothoracic horns, a lateral pair ..... *L. anomala*
- 2 (1) Four cephalothoracic horns, a dorsal pair and a ventral pair ..... 3
- 3 (4) Dorsal and ventral horns about the same size ..... *L. cruciata*
- 4 (3) Ventral horns much smaller than the dorsal ..... 5
- 5 (6) Dorsal horns simple and undivided ..... *L. tenuis*
- 6 (5) Dorsal horns distinctly forked ..... *L. cyprinacea*

## SUMMARY

Four genera and 12 species of parasitic Copepoda are reported from 12 genera and 17 species of Louisiana fish.

The species of *Ergasilus* are the most widely distributed and numerous of the parasitic copepods in these fish. Of these *E. versicolor* is the most prevalent.

*Ictalurus furcatus*, the blue cat, is host to the most species of parasitic copepods among the fish examined, one from each of the four parasitic genera found. The various bass are next; *Micropterus punctulatus*, the Kentucky bass, and *M. salmoides*, the largemouth bass, with three species each.

No marked host specificity is evident. *Ergasilus versicolor* appeared in 8 different species of fish, while *Lernaea anomala* and *L. cruciata* were in three different species respectively.

## REFERENCES

- HARDING, J. P. 1950—On some species of *Lernaea*. Bull. Brit. Mus. (Nat. Hist.) Zool. 1(1):1-27.
- MEEHEAN, O. L. 1940—A review of the parasitic crustacea of the genus *Argulus* in the collections of the United States National Museum. Proc. U. S. Nat. Mus. 88(3087):459-522.
- WILSON, C. B. 1911—North American parasitic copepods belonging to the family Ergasilidae. *Ibid.* 39(1788):263-400.
- 1914—Copepod parasites of fresh-water fishes and their economic relations to mussel glochidia. Bull. U. S. Bur. Fish. 34:331-374.
- 1917—The economic relations, anatomy, and life history of the genus *Lernaea*. *Ibid.* 35:165-198.
- 1944—Parasitic copepods in the United States National Museum. Proc. U. S. Nat. Mus. 94(3177):529-582.

## Endogenous Twenty-Four Hour Rhythms of Locomotor Activity and Oxygen Consumption in the Crawfish *Orconectes clypeatus*<sup>1</sup>

Milton Fingerman and Argimiro D. Lago

Newcomb College, Tulane University, New Orleans, Louisiana

Twenty-four hour rhythms of metabolic rate and locomotor activity have been observed in several crustaceans. Kalmus (1938) described a 24-hour locomotor activity rhythm in the crawfish *Astacus astacus*. The animal exhibited greater activity between 4 P.M. and midnight than at other times of day. By contrast, for several days after eyestalk ablation the *Astacus* were highly active throughout the 24-hour day and did not exhibit a 24-hour locomotor rhythm. Approximately 10 days after removal of the eyestalks the spontaneous locomotor activity of *Astacus* decreased to a level of very little activity at any time of day.

Roberts (1941) observed a 24-hour locomotor activity rhythm in the crawfish *Orconectes virilis*. The rhythm disappeared in darkness. Eyestalkless specimens of this species also did not exhibit a locomotor activity rhythm. In constant darkness eyestalkless crawfish were recorded in fewer and shorter rest periods indicating that the animals were more active than normal.

Schalleck (1942) observed 24-hour spontaneous locomotor activity rhythms in the crawfishes *Orconectes virilis*, *Procambarus clarki*, and *Cambarus diogenes*, kept in constant darkness. He described three types of individuals in each species. One type was more active at midnight than at other times of day, the second was more active at noon than at other times of day, and the third type was more active at dawn and dusk than at other times of day. In general, specimens of the three species were more active at night than during the day. Eyestalkless individuals were continually active and showed no rhythm of locomotor activity.

Edwards (1950) described 24-hour rhythms of metabolic rate and spontaneous locomotor activity in the fiddler crabs *Uca pugilator*, *U. pugnax*, and *U. minax*. Their oxygen consumption was normally higher at night than during the daytime. The 24-hour cycle of locomotor activity closely corresponded with the cycle of oxygen consumption. Brown, Bennett, and Webb (1954) described in detail the endogenous 24-hour rhythms of oxygen consumption in the fiddler crabs *U. pugilator* and *U. pugnax*. The maximum oxygen consumption of specimens of both species occurred at 6-8 A.M. A second lesser maximum was found about 10-11 P.M. The minimum oxygen consumption occurred about noon and a lesser minimum occurred about midnight. Eyestalkless *U. pugilator* also exhibited a persistent 24-hour rhythm of metabolic rate that differed slightly in form from that of normal indi-

<sup>1</sup> This investigation was supported by Grant No. B-838 from the National Institutes of Health.

viduals. Obviously, the eyestalk, contrary to earlier opinion, is not essential to the basic mechanism of 24-hour rhythmicity.

Fingerman (1955) demonstrated 24-hour rhythms of metabolic rate in both normal and eyestalkless dwarf crawfishes, *Cambarellus shufeldti*. The form of the rhythm was quite similar in both normal and eyestalkless *Cambarellus* and differed only slightly from the form of the rhythm described in fiddler crabs by Brown, Bennett, and Webb (1954). The oxygen consumption was maximal about 6 A.M. with a secondary maximum about 3-6 P.M. Minima occurred from 9 A.M. to noon and from 9 P.M. to midnight. Lowe (unpublished data) has observed that *Cambarellus* is most active in the laboratory about 7 A.M.

The life history and ecology of the crawfish *Orconectes clypeatus* have been described by Smith (1953). *Cambarellus shufeldti* and *Orconectes clypeatus* can be found occupying the same habitats. The present investigation was undertaken, therefore, to determine if *O. clypeatus* also exhibits 24-hour rhythms of oxygen consumption and locomotor activity.

#### MATERIALS AND METHODS

Adult specimens of the crawfish *Orconectes clypeatus* were collected every second week for eight weeks beginning January, 1956, in the vicinity of Hickory, Louisiana, for use in these experiments. The stock supply of crawfishes was kept in aquaria containing aerated tap water one inch deep under a constant illumination of 30 ft-c light intensity.

The locomotor activity of *Orconectes* was recorded under an illumination of less than one ft-c light intensity through use of the method described by Kalmus (1938). A thread was tied about a crawfish where the abdomen joins the cephalothorax. The thread was then tied to a light aluminum lever recording movements of the crawfishes on carbonized paper glued to the drum of a 24-hour kymograph. The drum rotated at the rate of 2.00 cm per hour. The kymograph drum was large enough to accommodate the records of three crawfishes simultaneously. The crawfishes were placed in small finger bowls containing fine gravel for traction and aerated tap water. Recording of the activity was initiated between 10 A.M. and 4 P.M. Twenty-four hours later the records were removed from the kymograph drum and sprayed with "Krylon" fixative. Hour intervals were then marked on the records and the movements for each hour counted. Since all the records were not initiated at the same hour of day and records of the activity throughout the same 24-hour period were desired, the data were rearranged so that in the activity graphs presented below (figs. 2, 3, 5, and 6) the data are presented on the basis of midnight to midnight values. In these figures the movements per hour have been plotted versus the hour of day. No matter what time of day the recording began, the number of movements from 11 P.M. to midnight were counted first and the activity for the remaining 23 hours were recorded in sequence. This method of recording the data 1) facilitated comparison of the locomotor activity of individual crawfish and 2) allowed data obtained with several individuals to be averaged. The data for each two hour interval beginning at 11 P.M. were averaged. Each point in figs. 2, 3, 5, and 6 represents the average of two hours of activity.

Oxygen consumption was recorded for periods longer than 24 hours by means of a continuously-recording respirometer designed by Brown (1954). Each respirometer consisted of a collapsible plastic bag attached to a 100 ml Soxhlet flask via a capillary connection. The plastic bag contained sufficient oxygen for at least three days. Weights were affixed to the exterior of the flask so that the respirometer would sink just below the surface of the water in a constant-temperature bath maintained at 29.0°C. As the crawfish consumed the oxygen, the volume of the plastic bag decreased, the specific gravity of the respirometer increased, and the buoyancy decreased. The respirometer, therefore, sank deeper. Increase in specific gravity was recorded by means of a lever system attached to ink pens recording on a drum that turned at the rate of 2.05 cm per hour. Decrease of the volume of oxygen in the respirometer caused the pen to trace a line continually moving closer to a fixed base line. The respirometer increased one gram in weight for each milliliter of oxygen consumed. Therefore, the lever system could be calibrated and the volume of oxygen per hour calculated. The method of analysis and presentation of the data were the same as described in detail by Brown, Bennett, and Webb (1954), Sandeen, Stephens, and Brown (1954) and Fingerma (1955).

The following were placed into each of 10 flasks for each determination of metabolic rate: a vial of 20 percent potassium hydroxide (carbon dioxide absorbent), a vial of saturated cupric chloride (ammonia absorbent), and a volume of aerated tap water sufficient to allow an *Orconectes clypeatus* to swim. Nine of the respirometers had one crawfish in each of them, the tenth served as a control. Only about 50 percent of the records were useable because some crawfish would die in the respirometers or the pens would fail during the night. The respirometers were maintained under constant illumination in a windowless room. The light intensity at the surface of the water in the constant temperature bath was 25 ft-c.

After removal from the respirometer the weight and sex of each crawfish were determined. The total wet weight was obtained by first blotting each crawfish in paper towelling to remove as much of the external liquid as possible and then weighing the animal to the nearest one-hundredth of a gram by means of an analytical balance. The rates of oxygen consumption were expressed as milliliters of oxygen consumed per gram of crawfish per hour (ml/g/hr). The 24-hour records of oxygen consumption were determined from 11 P.M. of one day until midnight of the following day. Data for each two-hour interval beginning at 11 P.M. were averaged. Each point in figs. 7-10 represents the average oxygen consumption over a two-hour period.

#### EXPERIMENTS AND RESULTS

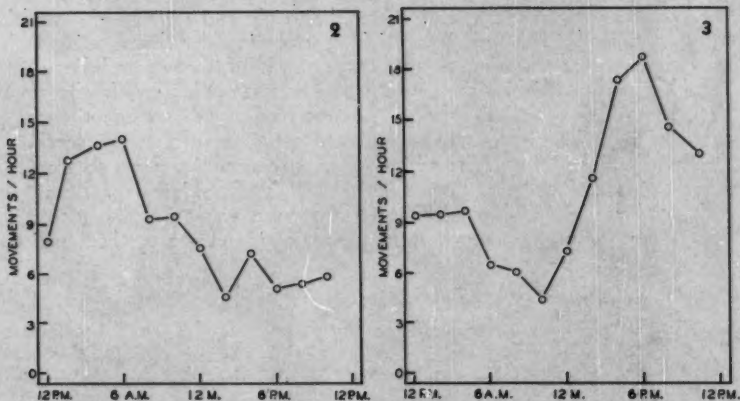
*Twenty-four hour rhythm of locomotor activity of normal Orconectes clypeatus.*—The locomotor activity of intact adult specimens of *O. clypeatus* was determined for 24-hour periods. A 24-hour rhythm of locomotor activity was evident from inspection of the kymograph records (fig. 1A, B). The kymograph records run from right to left.

Two distinct types of records were obtained. One type was produced by crawfish more active between midnight and noon than between noon and



Fig. 1.—Twenty-four hour locomotor activity records of normal *Orconectes clypeatus*. A, kymograph record of an individual more active from midnight to noon; B, kymograph record of an individual more active from noon to midnight; C, kymograph record of an individual maintained under constant illumination for three weeks that had lost its activity rhythm. In A and B noon is at the beginning and end of the records; in C 1:30 P.M.

midnight (fig. 1A.) The second type was produced by crawfish more active between noon and midnight than between midnight and noon (fig. 1B). Crawfishes more active between midnight and noon will be referred to as type A individuals; crawfishes more active between noon and midnight will be referred to as type B. The amplitude of the activity rhythm gradually diminished in specimens kept in the laboratory under constant illumination. After approximately three weeks in the laboratory most specimens showed no



Figs. 2, 3.—2. The 24-hour locomotor activity rhythm of normal *Orconectes clypeatus* more active from midnight to noon than from noon to midnight (type A). 3. The 24-hour locomotor activity rhythm of normal *O. clypeatus* more active from noon to midnight than from midnight to noon (type B).



activity as evidenced by the records (fig. 1C). The type individual (A or B) could not be determined prior to investigation.

The data obtained with intact type A specimens have been presented in fig. 2. This figure represents the average of 12 individuals. The data obtained with 15 type B individuals are presented in fig. 3. No correlation between the sex of the individual and the type of rhythm was evident, nor was there indication that a type A individual would become type B or vice versa.

Activity records of type A and type B individuals were obtained in the same 24-hour interval. The curves of figs. 2 and 3 show some basic similarities. The maxima of figs. 2 and 3 are 12 hours apart, at 6 A.M. (type A) and 6 P.M. (type B). In both curves there is indication of a secondary maximum about 12 hours after the primary maximum. Minimum activity occurred about noon. A lesser minimum was evident about midnight.

*Twenty-four hour rhythms of locomotor activity of eyestalkless Orconectes clypeatus.*—Twenty-four hour locomotor activity was determined in the manner described above for crawfishes whose eyestalks had been removed by transection at their bases at least 24 hours prior to use. Three types of records were obtained and are shown in fig. 4. In figure 4A is shown the type of record typical of eyestalkless crawfishes. These crawfishes were hyperactive as evidenced by more movements per hour than found in the records of normal *Orconectes*. Analysis of the records revealed that eyestalkless specimens possess a 24-hour locomotor activity rhythm in spite of their hyperactivity.

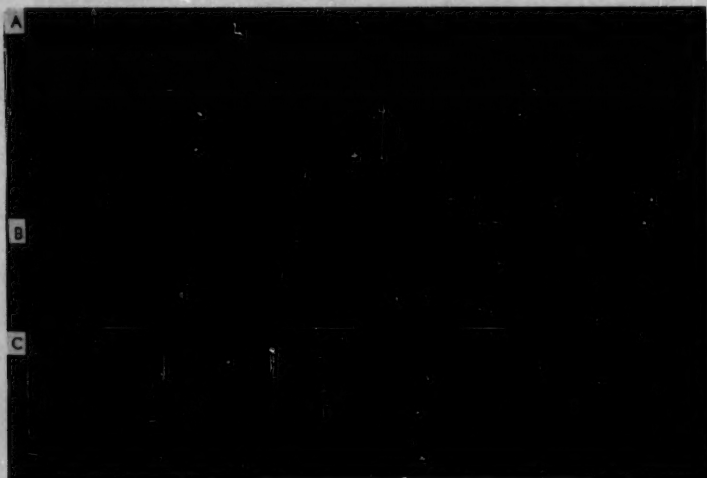
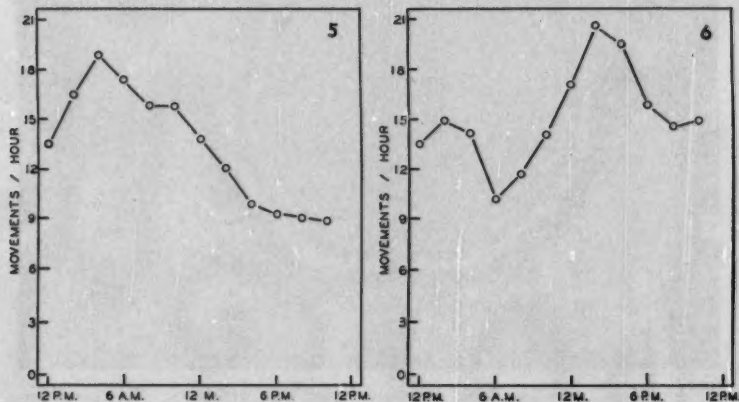


Fig. 4.—Twenty-four hour records of eyestalkless crawfishes. A, kymograph record of a hyperactive crawfish with higher activity from midnight to noon (type A); B, kymograph record of a hypoactive crawfish with higher activity from midnight to noon (type A); C, kymograph record of a crawfish whose constant activity obliterated all indication of a 24-hour locomotor activity rhythm. In A and B noon is at the beginning and end of the records; in C 1:30 P.M.

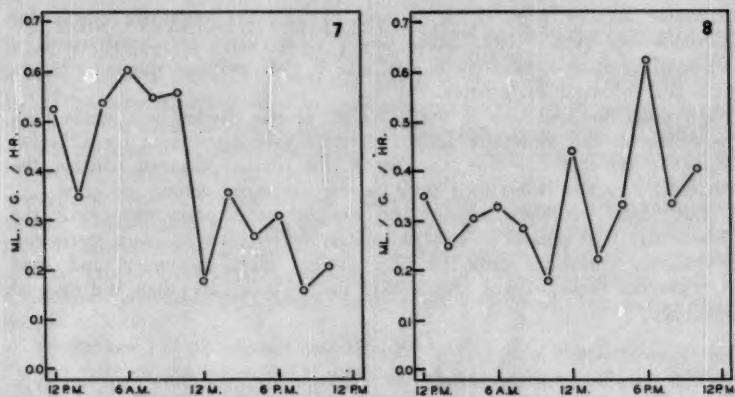
Eyestalkless crawfishes also exhibited the two types of locomotor activity rhythm (A and B) found with normal crawfishes. In fig. 4A is shown the kymograph record of a hyperactive type A eyestalkless crawfish. In fig. 4B is shown the locomotor activity record of another type A eyestalkless crawfish that was rhythmical although hypoactive as compared with normal crawfishes. Few of the eyestalkless specimens were hypoactive. In fig. 4C is shown the third type of locomotor activity record obtained with eyestalkless *Orconectes*. This individual was hyperactive at all times of day and night to such an extent that all evidence of a 24-hour locomotor activity rhythm had been obliterated. Two of the 25 eyestalkless individuals whose locomotor activity was recorded were of the type shown in fig. 4C.

The movements per hour were counted and averaged by two-hour periods for the types A and B eyestalkless *Orconectes*. The results are presented in figs. 5 (type A) and 6 (type B). Fig. 5 represents the average movements per hour of 15 eyestalkless crawfishes and fig. 6 the average movements per hour of eight crawfishes. As is evident from figs. 5 and 6 the same two types of 24-hour spontaneous locomotor activity rhythms found in normal specimens were evident in eyestalkless *Orconectes clypeatus*.

*Twenty-four hour rhythms of oxygen consumption in normal and eyestalkless Orconectes clypeatus.*—The oxygen consumption of normal and eyestalkless *Orconectes clypeatus* was determined from 11 P.M. of one day until midnight of the following day. Analysis of the data revealed that both normal and eyestalkless *Orconectes* exhibit 24-hour rhythms of oxygen consumption (figs. 7-10). Normal and eyestalkless crawfishes exhibited both types of rhythm that were observed in the rhythms of spontaneous locomotor activity. Some crawfishes used more oxygen between midnight and noon than between noon and midnight (type A), others used more oxygen between noon and midnight than between midnight and noon (type B).



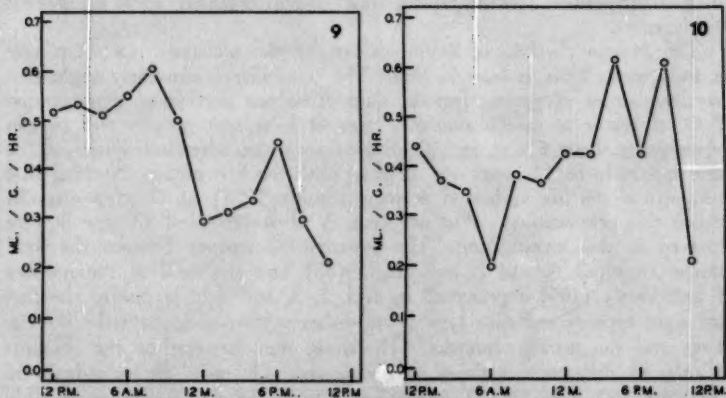
Figs. 5, 6.—5. The 24-hour locomotor activity rhythm of eyestalkless *Orconectes clypeatus* more active from midnight to noon than from noon to midnight (type A). 6. The 24-hour locomotor activity rhythm of eyestalkless *O. clypeatus* more active from noon to midnight than from midnight to noon (type B).



Figs. 7, 8.—7. The 24-hour rhythm of oxygen consumption of normal *Orconectes clypeatus* that had a higher metabolic rate between midnight and noon than between noon and midnight (type A). 8. The 24-hour rhythm of oxygen consumption of normal *O. clypeatus* that had a higher metabolic rate between noon and midnight than between midnight and noon (type B).

In fig. 7 is shown the curve obtained from the averaged data of 20 type A normal crawfishes. In fig. 8 is the 24-hour pattern of oxygen consumption of 13 type B normal crawfishes. In fig. 9 is shown the 24-hour rhythm of 12 type A eyestalkless *Orconectes*. In fig. 10 is depicted the 24-hour rhythm of 10 type B eyestalkless *Orconectes*.

There is a striking similarity between the character of the curves of



Figs. 9, 10.—9. The 24-hour rhythm of oxygen consumption of eyestalkless *Orconectes clypeatus* that had a higher metabolic rate between midnight and noon than between noon and midnight (type A). 10. The 24-hour rhythm of oxygen consumption of eyestalkless *O. clypeatus* that had a higher metabolic rate between noon and midnight than between midnight and noon (type B).

locomotor activity (figs. 2, 3, 5, and 6) and the respective curves for metabolic rate (figs. 7-10). Seven of the eight curves are characterized by two maxima at approximately 6 A.M. and 6 P.M. and two minima close to noon and midnight respectively.

In order to determine if the character of the rhythm was stable both the metabolic and locomotor activity patterns were determined for 17 crawfishes. In no case had the character of the rhythm changed whether the metabolic rate was determined prior to the locomotor activity or after.

Both total locomotor activity and oxygen consumption throughout the 24-hour day were greater in eyestalkless *Orconectes* than in intact specimens. Eyestalkless crawfishes exhibited 62.1 percent more movement and used 11.5 percent more oxygen throughout the 24-hour day than did normal crawfishes.

#### DISCUSSION

The population of the crawfish *O. clypeatus* exhibits more than one type of locomotor activity rhythm just as was found in the crawfishes *O. virilis*, *Procambarus clarki*, and *Cambarus diogenes* (Schalleck, 1942). However, the forms of the rhythms described by Schalleck did not correspond to the rhythms found in *Orconectes clypeatus*. No one who has investigated locomotor activity in crawfishes (Kalmus, 1938; Roberts, 1941; and Schalleck, 1942) has found a rhythm in eyestalkless crawfishes.

The center of endogenous 24-hour rhythmicity of *O. clypeatus* obviously does not reside in the eyestalk. Since the crawfishes used in the investigation of Schalleck (1942) were continually active after eyestalk removal, he postulated that 1) the eyestalks contained an inhibitory nervous center for locomotor activity and 2) the locomotor activity rhythm of normal crawfishes was due to rhythmical functioning of this inhibitory center. Obviously no such hypothesis could explain the results obtained with eyestalkless *O. clypeatus*.

The 24-hour rhythms of locomotor activity and metabolic rate must have an endogenous basis at least in part. The possibility is extremely slight that the same set of exogenous factors could cause one portion of a population of *O. clypeatus* to exhibit maximal rates of locomotor activity and oxygen consumption about 6 A.M. and simultaneously cause other individuals of the same species to be 12 hours out of phase with the first group. Nothing that is known of the life cycle and ecology (Smith, 1953) of *O. clypeatus* can explain this phenomenon. Fifty-one type A *Orconectes* and 37 type B were observed in this investigation. The apparent discrepancy between the total number of types A and B individuals (88) and the total of the number of individuals (105) represented by figs. 2, 3, and 5-10 is due to the fact that eight type A and nine type B crawfishes were used in both the respirometer and the activity recorder. Therefore, the character of the rhythms of only 88 different crawfishes were observed. Of these 88 individuals 51 (57.9 percent) were type A indicating that the population consists roughly of equal numbers of types A and B individuals.

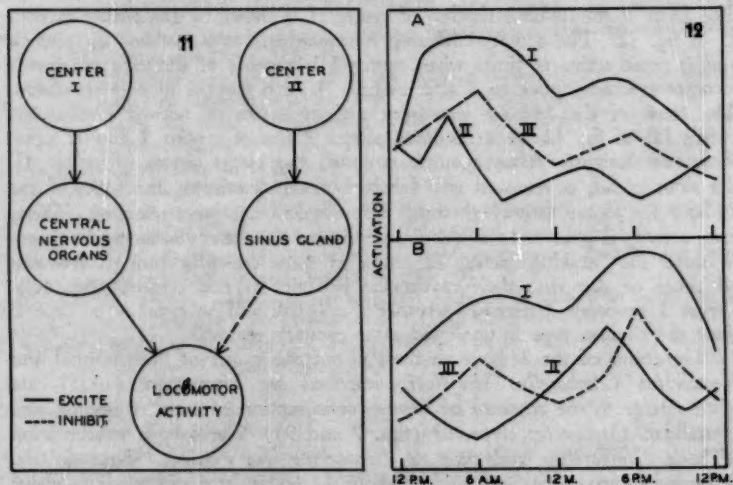
As is evident from inspection of figs. 2, 3, and 5-10, a secondary maximum was more evident in the four curves shown for type B crawfishes (figs. 3, 6, 8, and 10) than in the curves of type A crawfishes (figs. 2,

5, 7, and 9). Evidently, crawfishes which are most active in the early morning hours (type A) do not tend to be active in the evening. On the other hand, crawfishes which are extremely active in the evening (type B) tend to exhibit considerable activity in the early morning hours as well as in the evening. The same is true of the oxygen consumption of types A and B.

Maximal rates of locomotor activity and oxygen consumption of type A *Orconectes* occurred at 6 A.M. and at 6 P.M. for type B. However, in eyestalkless type A *Orconectes* the maximal rates of locomotor activity and oxygen consumption occurred at 4 A.M. and 8 A.M. respectively and for type B specimens at 2 P.M. and 4 P.M. respectively. Maximal locomotor activity preceded maximal oxygen consumption in both types A and B eyestalkless crawfishes. Evidently after eyestalk removal, metabolism lags behind activity.

Scudamore (1947) showed that removal of the sinus glands from within the eyestalks of the crawfish *O. immunis* led to an increase in the rate of oxygen consumption. The metabolic rate of dwarf crawfishes, *Cambarellus shufeldti*, also increases after eyestalk removal (Fingerman, 1955). Eyestalk extracts decreased the metabolic rates of both *Orconectes immunis* and *Cambarellus shufeldti*. These results have led to the conclusion that the eyestalk contains a hormone which lowers the metabolic rate of crawfishes. Scudamore (1947) also demonstrated that extracts of central nervous organs increased the metabolic rate of *Orconectes immunis*. Roberts (1941) found that eyestalk extracts of *O. virilis* inhibited locomotor activity.

An hypothesis devised to elucidate the probable mechanism of 24-hour



Figs. 11, 12.—11. Diagrammatic representation of an hypothesis to account for the 24-hour locomotor activity rhythm of *Orconectes*. See text for complete explanation. 12. Diagrammatic representation of the manner in which the rhythmical mechanism presented in Figure 11 operates. A, type A *Orconectes*; B, type B *Orconectes*. See text for complete explanation.



rhythmicity in *Orconectes clypeatus* has been diagrammatically represented in figures 11 and 12. The data on the endocrine control of metabolic rate (Scudamore, 1947; Fingerman, 1955) may equally well be interpreted by postulating that the eyestalk contains a hormone which lowers locomotor activity and that the central nervous system elaborates a principle which increases locomotor activity. Concomitant with increase and decrease of locomotor activity is a corresponding increase or decrease of oxygen consumption in order to compensate for the increased locomotor activity.

Two centers of rhythmicity are postulated to explain the character of the 24-hour rhythm of locomotor activity just as two centers of rhythmicity were postulated by Brown and Webb (1949) to account for the characteristics of modifiability of the 24-hour rhythmicity of color change in the fiddler crab *Uca pugnax*. Center I, the primary center of 24-hour rhythmicity, is located within the supraesophageal ganglia and activates neurosecretory cells within the central nervous system. These neurosecretory cells produce a hormone which induces increased locomotor activity (fig. 11). The form of the endogenous rhythm of center I is illustrated by curve I in fig. 12 and is quite similar to the curves of activity found in eyestalkless *Orconectes* (figs. 5 and 6). Center I causes general locomotor activity throughout the 24-hour day with a maximum at either 6 A.M. or 6 P.M.

Center II, located either in the central nervous system or in the nervous tissues of the eyestalk, has an inherent 24-hour rhythmicity of its own. In contrast to center I, center II acts upon the sinus gland causing the gland to secrete a hormone which inhibits locomotor activity (fig. 11). The form of the 24-hour rhythm of center II is shown by the curves marked II in fig. 12. The activity-inhibiting hormone acts as a "brake" on activity and is most active at times when center I is capable of inducing maximum locomotor activity prior to 5 A.M. in type A or 6 P.M. in type B crawfishes. The form of the 24-hour locomotor activity curve of normal *Orconectes*, curves III of fig. 12 are a resultant of the effects of centers I and II upon locomotor activity. After eyestalk removal, the target organ of center II, the sinus gland, is removed and center I alone determines the form of the 24-hour locomotor activity rhythm. The "brake" has been removed. Therefore, activity is governed solely by center I and the activity-inducing hormone. Without the "braking" action of center II some crawfishes are so active at all times of day that their rhythmical behavior is not evident (fig. 4C). Center I probably determines whether a crawfish will be type A or type B since the rhythm type is unaltered after eyestalk removal.

The forms of the 24-hour rhythms of metabolic rate of both normal and eyestalkless *Cambarellus shufeldti*, described by Fingerman (1955) are quite similar to the rhythms of oxygen consumption of type A normal and eyestalkless *Orconectes clypeatus* (figs. 7 and 9). The oxygen consumption of both *Cambarellus* and type A *Orconectes* was maximal about 6 A.M. A secondary maximum was evident about 12 hours later with minima about noon and midnight.

#### CONCLUSIONS

Spontaneous locomotor activity and oxygen consumption of the crawfish *Orconectes clypeatus* have been continuously recorded for 24-hour periods.

Analysis of the data revealed 24-hour rhythms of both spontaneous locomotor activity and metabolic rate.

The population consisted of approximately equal numbers of two types of individuals. One type exhibited more locomotor activity and had a higher metabolic rate between midnight and noon than between noon and midnight (type A). The second type exhibited higher locomotor activity and a higher metabolic rate between noon and midnight than between midnight and noon (type B).

Eyestalkless *O. clypeatus* also exhibited 24-hour rhythms of locomotor activity and metabolic rate. Eyestalkless crawfishes were on the average more active and had a higher metabolic rate than intact crawfishes.

Eyestalkless crawfishes exhibited the same two types, A and B, of rhythms of locomotor activity and metabolic rate found in intact *Orconectes*.

Rates of locomotor activity and oxygen consumption were maximal about 6 A.M. in group A and about 6 P.M. in group B. The curves depicting locomotor activity and metabolic rate tended to be bimodal. A secondary maximum occurred approximately 12 hours after the primary peak. Minima generally occurred about noon and midnight. The secondary maximum was more evident in type B than in type A *Orconectes*.

In an attempt to explain these results, an hypothesis based on the existence of two centers of rhythmicity in *Orconectes clypeatus* has been presented. Each center has a 24-hour rhythmicity of its own. One center has an excitatory effect upon locomotor activity; the second has an inhibitory effect.

#### REFERENCES

- BROWN, F. A., JR. 1954—A simple, automatic, continuous-recording respirometer. *Rev. Sci. Instruments* 25:415-417.
- , M. F. BENNETT, AND H. M. WEBB 1954—Persistent daily and tidal rhythms of oxygen consumption in fiddler crabs. *J. Cell. Comp. Physiol.* 44:477-506.
- AND H. M. WEBB 1949—Studies of the daily rhythmicity of the fiddler crab, *Uca*. Modifications by light. *Physiol. Zool.* 22:136-148.
- EDWARDS, G. A. 1950—The influence of eyestalk removal on the metabolism of the fiddler crab. *Physiol. Comp. et Oecol.* 3:34-50.
- FINGERMAN, M. 1955—Factors influencing the rate of oxygen consumption of the dwarf crayfish, *Cambarellus shufeldtii*. *Tulane Stud. Zool.* 3:103-116.
- KALMUS, H. 1938—Das Aktogramm des Flusskrebes und seine Beeinflussung durch Organextrakte. *Zeit. vergl. Physiol.* 25:798-802.
- ROBERTS, T. W. 1941—Evidence that hormonal inhibition of locomotion occurs for the crayfish *Cambarus virilis* Hagen. *Anat. Rec. (Suppl.)* 81:46-47.
- SANDEEN, M. I., G. C. STEPHENS, AND F. A. BROWN, JR. 1954—Persistent daily and tidal rhythms of oxygen consumption in two species of marine snails. *Physiol. Zool.* 27:350-356.
- SCHALLECK, W. 1942—Some mechanisms controlling locomotor activity in the crayfish. *J. Exp. Zool.* 91:155-166.
- SCUDAMORE, H. H. 1947—The influence of the sinus glands upon molting and associated changes in the crayfish. *Physiol. Zool.* 20:187-208.
- SMITH, E. W. 1953—The life history of the crayfish *Orconectes (Faxonella) clypeatus* (Hay). *Tulane Stud. Zool.* 1:79-96.

# A Study of the Population of Emerging and Littoral Insects Trapped as Adults from Tributary Waters of the Thames River at London, Ontario<sup>1</sup>

W. W. Judd<sup>2</sup>

University of Western Ontario, London

During the summer of 1952 the writer (Judd, 1954) conducted a survey of mosquitoes and during 1953 a survey of calyptate flies of medical importance (Judd, 1956) in the vicinity of London, Ontario. As a third contribution to the study of insects in the vicinity of London it was decided to conduct a study of the insects occurring in bodies of water tributary to the Thames River at London in 1954. The present paper is a report on this project.

*Acknowledgment.*—The writer gratefully acknowledges the assistance of Miss A. M. Gerhardt who aided throughout the summer of 1954 in collecting insects from traps, in sorting and counting specimens and in recording data. Much of the data were assembled during the summer of 1956 while the writer held a Summer Research Associateship of the National Research Council of Canada.

## DESCRIPTION OF COLLECTION SITES

The sites at which collections were made were five bodies of water tributary to the Thames River at London (fig. 1). The "North Branch" and the "South Branch" of the Thames meet near the center of the City of London, their point of confluence being known locally as the "Forks of the Thames." Thence the Thames River flows westward from London to the Great Lakes. Collection sites 1 and 2 were located on tributaries of the North Branch, sites 3 and 4 on a backwater of the Thames River west of the forks and site 5 on a tributary of the South Branch, as detailed in the following account.

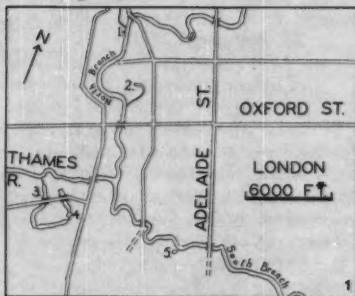


Fig. 1.—Map of London, Ontario, showing location of collections sites 1-5.

*Site 1.*—This was a pool about thirty feet in diameter, roughly circular in outline and joined to the North Branch by a narrow ditch. Its bottom and sides consisted of coarse gravel. It was subject to frequent scouring in spring owing to flood waters passing through it as they swept around an

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<sup>2</sup> Associate Professor of Zoology.

abrupt bend in the river just north of the pool. Consequently there was little permanent vegetation in the pool or around its immediate border. Creeping plants of moneywort (*Lysimachia nummularia* L.) were present on the bank of the pool, a scattered accumulation of duckweed (*Lemna minor* L.) was on its surface and a sparse growth of waterweed (*Elodea canadensis* Michx.) grew in the water. This was pool A1 in the mosquito survey conducted in 1952 (Judd, 1954).

Site 2.—This was a long, narrow tributary pond of the North Branch in Gibbons' Park, a public park of the city. The water was stagnant and the bottom of the pool was covered with a foot or more of thick, black, organic muck. The bank of the pond supported a luxurious growth of arrowhead (*Sagittaria latifolia* Willd.), water hemlock (*Cicuta bulbifera* L.), white vervain (*Verbena urticifolia* L.), boneset (*Eupatorium perfoliatum* L.) and jewelweed (*Impatiens capensis* Meerb.). Clumps of cat-tail (*Typha latifolia* L.) grew along the edge of the pond, tangled masses of hornwort (*Ceratophyllum demersum* L.) were submerged in the water and by mid-summer the whole surface of the pool was covered solidly with floating plants of *Lemna minor* and water-meal (*Wolffia columbiana* Karst. and *W. punctata* Griesb.).

Site 3.—This was at the north-west end of a horseshoe-shaped backwater of the Thames locally known as "The Coves." At site 3 the water's edge was lined with plants of *Eupatorium perfoliatum*, *Impatiens capensis*, *Verbena urticifolia*, joe-pye-weed (*Eupatorium maculatum* L.), Canada anemone (*Anemone canadensis* L.) and swamp milkweed (*Asclepias incarnata* L.). There were no rooted or submerged plants in the water but a few fronds of *Lemna minor* floated on the surface. The water was stagnant and the bottom was covered with organic ooze mixed with fine silt. This was pool C1 in the mosquito survey (Judd, 1954).

Site 4.—This was a pool at the south-east extremity of The Coves. It was narrowed at its north and south ends and so was constricted off somewhat from the rest of The Coves as a circular pool. The water was stagnant and polluted by a flow of sewage from a nearby open sewage-drain and by run-off from a dump which formed its western border. Plants around its border included bur-reed (*Sparganium eurycarpum* Englm.), turtlehead (*Chelone glabra* L.) and water-plantain (*Alisma triviale* Pursh). The shallow water around its edge was occupied by stands of *Typha latifolia*, while submerged *Ceratophyllum demersum* formed tangled masses in the water. There was a sparse growth of *Lemna minor* on the surface. This was pool C6 in the mosquito survey (Judd, 1954).

Site 5.—This was a broad, shallow pond adjacent to the South Branch and polluted with industrial wastes from adjacent factories and by run-off from a dump along its south border. Its bottom was covered with thick, black, organic muck. A heavy growth of Canary-grass (*Phalaris arundinacea* L.) lined the banks of the pool and with it grew fringed loosestrife (*Lysimachia ciliata* L.). In the water were stands of *Typha latifolia* and clumps of water-dock (*Rumex verticillatus* L.). By mid-summer the surface of the pool was

solidly covered with a growth of *Lemna minor*. This was pool D2 in the mosquito survey (Judd, 1954).

#### METHODS

Insects were trapped in a tent-trap set out on the water at each of the five collection sites. The trap was a modification of that used for the same purpose by Miller (1941). It was built to enclose four square feet of water surface (fig. 2). The sides of a trap were four flat boards, five inches wide, nailed together so that the inside of the trap was 2 feet x 2 feet square. A square piece of plastic screening (no. 16 mesh) was nailed to the inside of the four sides with tacks and strips of masonite so that the screen formed a "tent" above the surface of the water. Two stiff wires, arching and crossing above the center of the screen, were nailed at the corners of the trap. The screen was suspended from the wires by short strings passed through the screen and tied to small sticks applied against the lower surface of the screen. The trap was supported on the water by two floats wired to opposite sides of the trap. Each float was an empty one gallon varnish tin painted with waterproof paint and with its lid soldered shut. The trap was kept in one position during the course of the investigation and was held there by a rope anchored at one end to bricks on the bottom of the pool and stapled at the other end to the side of the trap.



Fig. 2.—Tent-trap in position on pool.

A trap was set out on the water at each site on March 27 several feet from shore at such a distance that it could be reached by a collector wearing hip-length rubber boots. The traps were removed from the water on November 6. Each day the insects in the traps were collected. One side of the trap was raised above the surface of the water and an aspirator was passed into the trap and small insects were sucked into it. Larger insects, such as damsel-flies, were picked from the lower surface of the screen with the fingers. The insects so collected were put into a poison jar and taken to the laboratory for sorting, counting, pinning (or preserving in fluid) and labelling. The depth of the water at each trap was read each day until October 13 from a scale, graduated in inches, on the side of a stake driven into the bottom of the pool at each trap.

The depth of the water fluctuated most at Trap 1 owing to the sudden recurrent flooding of the pool by the North Branch in spring. On March 24 the pool was still frozen over. Thawing occurred by March 29 when the depth was 24 inches. The maximum depth (55 inches) occurred on April 22. Thereafter the water fell gradually to a depth of 3 inches by July 7 and then remained at 10 to 20 inches until September 15 after which it rose gradually to 27 inches by October 13. At Trap 2 the depth was 23 inches on March 24 and remained thereafter between 18 and 24 inches until



October 13. At Trap 3 the depth was 15 inches on March 24 and remained thereafter at 7 to 17 inches until October 13. At Trap 4 the depth was 18 inches on March 24 and during the summer the level fell gradually until by August 1 the trap was resting on the mud and was surrounded by a few inches of water only after rains. This condition prevailed until the middle of September when the water level rose and attained a depth of 12 inches by October 13. At Trap 5 the water depth was 17 inches on March 24 and increased to 31 inches on March 27. The level fell gradually to a minimum of 5 inches in the middle of August and thereafter was between 7 and 13 inches.

The following specialists in the taxonomy of the various groups of insects kindly identified the insects: F. P. Ide, University of Toronto (Ephemeroptera), E. M. Walker, Royal Ontario Museum, Toronto (Odonata), G. B. Wiggins, Royal Ontario Museum, Toronto (Trichoptera), L. A. Kelton, Systematic Entomology, Department of Agriculture, Ottawa (Hemiptera), R. deRuelle, Systematic Entomology, Department of Agriculture, Ottawa (Coleoptera), C. P. Alexander, University of Massachusetts, Amherst (Tipulidae), W. W. Wirth, United States Department of Agriculture, Washington (Tendipedidae), A. Stone, United States Department of Agriculture, Washington (*Chaoborus*), J. R. Vockeroth, Systematic Entomology, Department of Agriculture, Ottawa (Sciaridae, Stratiomyidae, Rhagionidae, Dolichopodidae, Chloropidae, Tetracercidae, Muscidae), G. E. Shewell, Systematic Entomology, Department of Agriculture, Ottawa (Empidae, Ephydriidae, Borboridae, Sarcophagidae, Tachinidae), W. R. M. Mason, Systematic Entomology, Department of Agriculture, Ottawa (Hymenoptera). The mosquitoes (Culicinae) were identified by the writer with the aid of keys in Matheson (1944), Bohart (1948) and Carpenter and LaCasse (1955).

All specimens are retained in the collections of the Department of Zoology, University of Western Ontario except as noted in the "Account of Species Collected," as follows: Canadian National Collection (CNC), United States National Museum (USNM), Royal Ontario Museum (ROM), University of Massachusetts (UM).

#### ACCOUNT OF TOTAL CATCH

The numbers of the various insects collected in the traps during the period of investigation are presented in table 1 and the numbers of insects of the seven orders collected in the traps are presented in table 2. During the whole period that the traps were in operation, March 27 to November 6, 9,152 insects were collected. Most of the insects were species whose larvae are aquatic and whose adults emerge from the water, but a few were insects which commonly dwell on emergent aquatic vegetation or in the littoral zone. The great majority of the insects (99.27 percent) were Diptera and among these the Tendipedidae predominated (93.7 percent). Next in point of numbers (5.3 percent) were the Culicidae. The other families of Diptera were present in smaller numbers, each accounting for a fraction of 1 percent of the total. The other orders of insects, Ephemeroptera, Odonata, Trichoptera, Hemiptera, Coleoptera and Hymenoptera likewise accounted for only a small fraction of the collection.

The most productive site was No. 3 at which the trap collected more than half (62.4 percent) of the total catch of insects. Here the midges predominated, as they did in most of the traps, and one species of mosquito, *Chaoborus punctipennis*, was prevalent. The next most productive site was No. 4 with the trap yielding 26.1 percent of the total. The greatest number

of biting midges (Heleidae) were caught in this trap and it was here that the only specimens of the mayfly, *Callibaetis fluctuans*, occurred. Trap 2 accounted for 7.5 percent of the total catch and here the predominant group was the Culicidae represented by four species (table 1) among which *Culex pipiens* was most numerous. At site 1 the trap collected 2.7 percent of the total collection. Here the midges predominated and most of the caddis-flies were caught. Representatives of all but two of the families of Diptera collected during the season were collected at this site. The least productive site was No. 5 at which only 0.3 percent of the insects were trapped. The Odonata, represented by the damsel-fly, *Ischnura verticalis*, was the only group that was present in greater numbers at this site than at any other.

### Account of Species Collected

#### EPHEMEROPTERA

##### HEXAGENIIDAE

*Hexagenia affliata* McD.—1 ♂ (Trap 1: August 2). Burks (1953) (treating it as a synonym of *munoa* Eaton) records that this species apparently normally develops in small lakes. It has been recorded from Ontario by Needham *et al.* (1935).

##### BAETIDAE

*Callibaetis fluctuans* Walsh.—2 ♂♂, 7 ♀♀ (Trap 4: September 9-15). These mayflies emerged in trap 4 at a time when the trap was resting on the mud and there was little water present. Usinger *et al.* (1956) include this species among mayflies which are still-water forms that climb amid vegetation. The conditions at trap 4 were of this type during the summer for the water was stagnant and masses of hornwort were present. The period of emergence is similar to that found for this species at Hamilton, Ontario (Judd, 1949, 1953).

#### ODONATA

##### COENAGRIIDAE

*Ischnura verticalis* (Say).—4 ♂♂, 6 ♀♀ (Trap 4: August 3—1, August 19—1; Trap 5: June 1 to June 21—8). The times of emergence of this species are in accord with the estimate of Walker (1953) that *I. verticalis* shows two peaks of abundance, a higher one in June and a lower one in August. Its presence at sites 4 and 5 is also in accord with Walker (1953) who records that it is found in permanent waters of almost any kind: ponds, ditches, etc.

##### AECHMIDAE

*Anax junius* (Drury).—1 insect (Trap 4: August 9). This dragonfly emerged when the trap was resting on the mud and no water surrounded it. Its date of emergence falls within the range of emergence dates found for this species at Hamilton (Judd, 1953).

#### TRICHOPTERA

##### HYDROPTILIDAE

*Hydroptila perdita* Morton.—1 ♂ (ROM) (Trap 3: July 23). Ross (1944) records this species from Ontario.

*Hydroptila* sp.—1 ♀ (ROM) (Trap 1: June 25).

##### HYDROPSYCHIDAE

*Cheumatopsyche (speciosa)* (Banks)?—4 ♀♀ (ROM) (Trap 1: August 13-August 25). Ross (1944) records that larvae of *Cheumatopsyche* occur in a wide variety of waters and that *C. speciosa* has a preference for large rivers.

##### PHILOPOTAMIDAE

*Chimarra obscura* (Walker).—1 ♀ (ROM) (Trap 1: August 16). Ross (1944) records this species from Ontario.

## HEMIPTERA

## SALDIDAE

*Saldula confluenta* (Say).—5 insects (Trap 1: June 18, July 14—2; Trap 2: August 10—1; Trap 3: June 17, 24—2). These bugs were found inside the traps on the woodwork or, in the case of trap 2, on the floating plants of *Lemna minor*. Saldids are typical inhabitants of beaches and shore lines (Usinger *et al.*, 1956).

*Saldula pallipes* Fabr.—5 insects (Trap 2: July 24—1; Trap 3: July 27—1; Trap 4: July 17—2, August 3—1).

*Saldula* sp.—4 insects (Trap 2: July 26—1, August 3—1, August 9—1; Trap 3: July 27—1).

## MESOVELIIDAE

*Mesovelia mulsanti* White.—6 insects (Trap 4: August 2—3, August 6—1, August 10—1, August 16—1). These bugs were found in trap 4 at a time when the trap was resting on the mud. Hoffman (1932) records that it lives upon the floating shoreward vegetation of ponds, marshes, etc.

## COLEOPTERA

## CARABIDAE

*Bembidion* sp.—18 beetles (Trap 2: July 11—1; Trap 3: July 13 to August 10—12; Trap 4: July 8 to July 30—4; Trap 5: September 12—1). Beetles of this genus inhabit the littoral zone of streams, lakes, ponds, etc. (Usinger *et al.*, 1952). Usinger *et al.* (1956) record that they share their microhabitat with bugs of the family Saldidae. One beetle was in Trap 3 on July 27 in company with specimens of *Saldula pallipes* and *Saldula* sp.

*Agonum* sp.—1 beetle (Trap 3: July 14). This beetle was collected from Trap 3 on the same day as a beetle of the genus *Bembidion*. Lindroth (1954, 1955) records that several species of *Agonum* are strongly hygrophilous, living at the margins of ponds and pools.

## CURCULIONIDAE

*Ceutorhynchus septentrionalis* Gyll.—1 beetle (Trap 2: May 19). McGaha (1952) and Usinger *et al.* (1956) record several species of weevils reared from aquatic plants but include none in the genus *Ceutorhynchus*. Blatchley and Leng (1916) report that *C. septentrionalis* feeds on wild mustard and other cruciferous plants. It is possible that the weevil in trap 2 was washed beneath the trap from outside and survived to climb up into the trap.

## DIPTERA

## TIPULIDAE

*Tipula furca* Walker.—1 fly (UM) (Trap 1: August 9). Leonard (1926) records this species, under the name *T. bella*, from several localities in New York, its seasonal range being from May to September.

*Erioptera caloptera* Say.—1 fly (UM) (Trap 4: August 4). Leonard (1926) records this species from New York, its seasonal range being from June to September.

## TENDIPEDIDAE

*Pentaneura illinoensis* (Mall).—1 ♂, 5 ♀♀ (1, USNM) (Trap 1: July 29—1, August 5—2; Trap 2: July 2—1; Trap 3: August 11—1; Trap 4: July 18—1).

*Pelopia punctipennis* (Mg.).—341 ♂♂, 291 ♀♀ (4, USNM) (fig. 3A) May 22—September 17, maxima July 6, August 17 (28, 31 insects). The great majority emerged in Traps 3 and 4 (table 1), very few in Trap 5 and none in Traps 1 and 2. The period of emergence corresponds closely to that for this species at Hamilton (May 18–September 29) (Judd, 1953).

*Clinotanytus flavicinctus* (Lw.).—1 ♂ (USNM) (Trap 4: August 23).

*Anatopynia dyari* (Coq.).—9 ♂♂, 7 ♀♀ (4, USNM) (Trap 2: June 10 to June 21—15, maximum June 15—8; Trap 5: June 15—1). Johannsen (1905) records breeding this species from larvae collected in pools at Ithaca, New York.

*Procladius culiciformis* L.—12 ♂♂, 16 ♀♀ (5, USNM) (fig. 3B) May 31-September 24. This was one of the scarcer midges in the collections. In this respect, and in its distribution through the season, it resembles the population of the same species at Hamilton (Judd, 1953).

*Procladius bellus* Loew.—21 ♂♂, 28 ♀♀ (4, USNM) (fig. 3C) May 25-September 8, maximum July 28 (6 insects). This species was collected at Hamilton (Judd, 1953).

*Orthocladius* sp.—1 ♂ (Trap 5: June 6). Several species of *Orthocladius* are recorded from New York state by Johannsen (1905).

*Hydrobaenus* spp.—67 ♂♂, 52 ♀♀ (5, USNM) (fig. 3D) April 12-September 13, maximum June 11 (12 insects). These midges were distributed through the five traps (table 1). Using *et al.* (1956) point out that midges of the genus *Hydrobaenus* are subaquatic and terrestrial and breed in damp and wet ground in various habitats.

*Cricotopus trifasciatus* (Panzer).—75 ♂♂, 6 ♀♀ (3, USNM) (fig. 3E) April 21-September 4, maximum June 25 (6 insects). This species emerged in traps 1, 3 and 4 (table 1). It was one of the commoner species collected at Hamilton (Judd, 1953).

*Cricotopus bicinctus* (Mg.).—196 ♂♂, 76 ♀♀ (6, USNM) (fig. 3F) April 23-October 8, maximum May 27, June 5 (26, 26 insects). Most of these midges emerged in Trap 3. This species is recorded from New York by Johannsen (1905).

*Polypedium fallax* (Joh.).—6 ♂♂, 18 ♀♀ (4, USNM) (fig. 3G) May 19-September 12, maximum June 3 (3 insects). This was one of the scarcer midges and was the only one of which the majority of specimens emerged in Trap 1 (table 1). It occurs at other localities in Ontario (Townes, 1945).

*Tanytarsus nigricans* (Joh.).—65 ♂♂, 37 ♀♀ (6, USNM) (fig. 3H) April 30-October 1, maximum July 14 (6 insects). Most of the midges emerged in Trap 4. The period of emergence corresponds closely to that found at Hamilton (Judd, 1953). It occurs at other localities in Ontario (Townes, 1945).

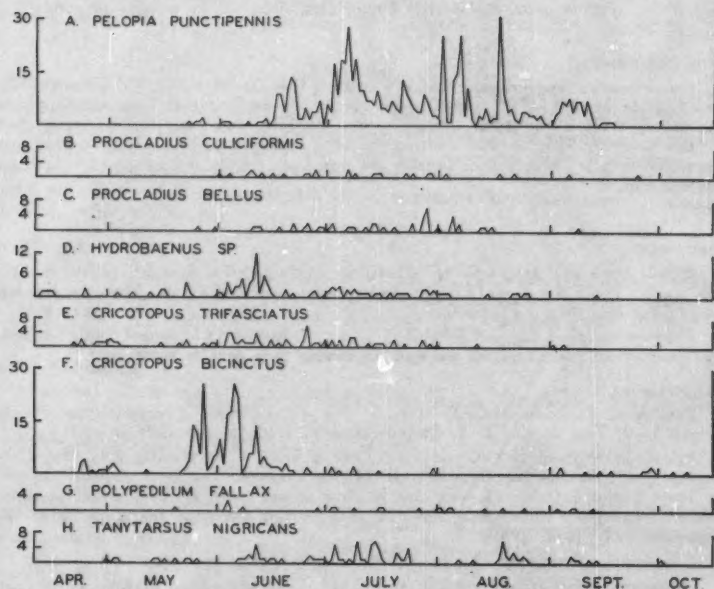


Fig. 3 (A-H).—Periods of emergence of adults of Tendipedidae.

*Tendipes decorus* (Joh.).—804 ♂♂, 772 ♀♀ (4, USNM) (fig. 4A) April 22–September 12, maximum July 27 (119 insects). This was one of the commonest midges in the collections. Most of them emerged in Trap 4 (table 1). It occurs at several localities in Ontario (Townes, 1945). Usinger *et al.* (1956) report that it occurs particularly in shallow, oxygen-deficient waters.

*Tendipes dux* (Joh.).—18 ♂♂, 8 ♀♀ (6, USNM) (fig. 4B) June 20–July 24, maximum July 2 (4 insects). This was one of the scarcer midges in the collections. Most of them emerged in Trap 2 (table 1).

*Tendipes plumosus* (L.).—1 ♂ (Trap 3: July 3). This species has been collected at several localities in Ontario (Townes, 1945). Townes (1945) records that the normal breeding place is soft mucky bottoms of eutrophic lakes, nearly always in depths below 4 meters. The bottom at Trap 3 was covered with organic ooze but the water level was never more than 24 inches.

*Glyptotendipes lobiferus* (Say).—2,450 ♂♂, 1,956 ♀♀ (5, USNM) (fig. 5) May 12–October 13, maximum July 17 (140 insects). This was the commonest emerging insect collected. Its seasonal distribution is similar to that at Hamilton (Judd, 1953) with maximum emergence in mid-July. There was, however, a larger fall emergence than at Hamilton. Townes (1945) records that it is common throughout the growing season, but more common in summer. Berg (1950) reports that it is found in burrows in stems of *Potamogeton*.

*Glyptotendipes brachialis* (Coq.).—81 ♂♂, 94 ♀♀ (6, USNM) (fig. 6A) May 22–September 13, maximum June 26 (9 insects). This species occurred only in Trap 3 and 4, predominantly in Trap 3 (table 1).

#### HELEIDAE

The biting midges were mostly unidentified but included some specimens in the genus *Culicoides*. Twenty-two midges emerged between May 26 and July 24.

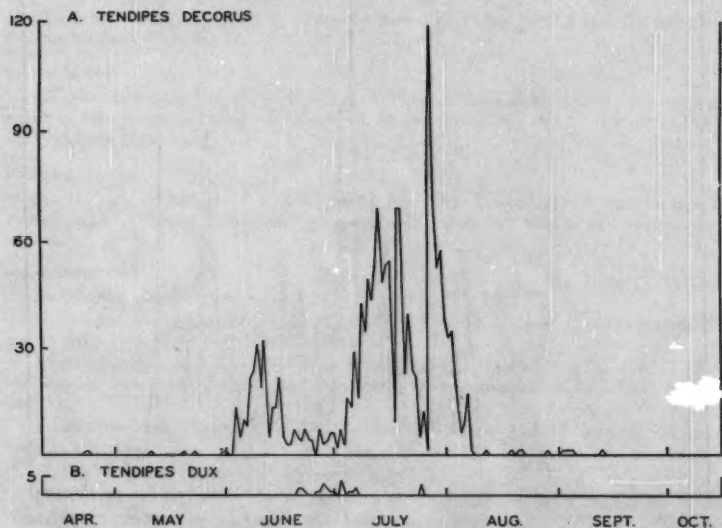


Fig. 4 (A-B).—Periods of emergence of adults of Tendipedidae.



## CULICIDAE

*Chaoborus flavicans* (Mg.).—28 ♂♂, 32 ♀♀ (4, USNM) (fig. 6C) June 15–August 22, maximum July 9 (22 insects). All these mosquitoes emerged in Trap 2 (table 1). Larvae of the genus *Chaoborus* are predacious on Crustacea and mosquito larvae (Howard *et al.*, 1912). No collections of Crustacea were made at site 2 but a large population of the mosquito, *Culex pipiens*, was present there (table 1).

*Chaoborus punctipennis* (Say).—66 ♂♂, 81 ♀♀ (4, USNM) (fig. 6B) June 13–September 3, maximum July 23 (21 insects). The great majority of these mosquitoes emerged in Trap 3.

*Anopheles punctipennis* (Say).—1 ♂ (Trap 1: October 6). This species was collected at London in 1952 (Judd, 1954). Carpenter and LaCasse (1955) record that larvae of this species are found in a large variety of aquatic habitats including ponds.

*Culex territans* Walker.—1 ♂, 1 ♀ (Trap 1: August 25; Trap 2: June 13). This mosquito was identified with keys in Bohart (1948) and Carpenter and LaCasse (1955). Several mosquitoes collected in the survey of 1952 (Judd, 1954) were identified as *C. apicalis* Adams by use of keys in Matheson (1944) who does not include *C. territans* in the North American fauna. A re-examination of the larvae collected and adults reared in 1952, using keys in Bohart (1948) and Carpenter and LaCrosse (1955), shows that mosquitoes included as *C. apicalis* (Judd, 1954) are properly referred to *C. territans*.

*Culex pipiens* L.—138 ♂♂, 131 ♀♀ (fig. 6D) May 22–August 28, maxima June 28, August 15 (16, 20 insects). These mosquitoes emerged only in Trap 2 (table 1). *C. pipiens* was collected at London in large numbers in 1952 (Judd, 1954).

*Culex restuans* Theobald.—4 ♂♂, 1 ♀ (Trap 2: June 10–2, July 8–3). This species was collected in 1952 (Judd, 1954).

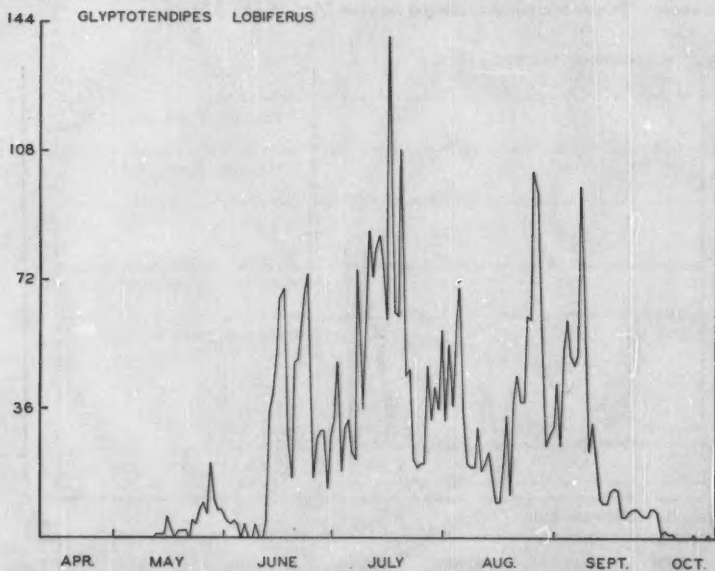


Fig. 5.—Period of emergence of adults of *Glyptotendipes lobiferus*.

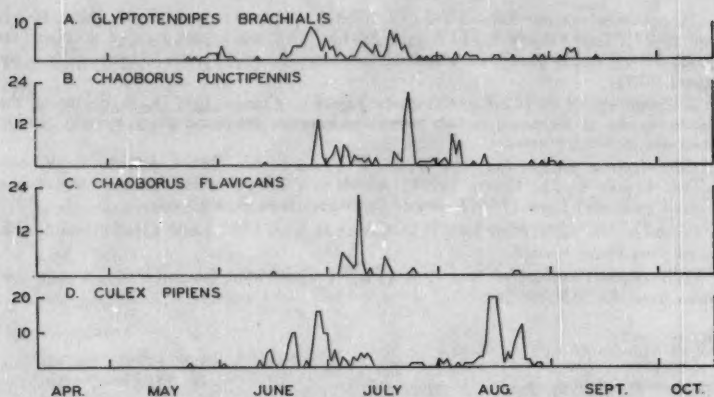


Fig 6 (A-D).—Periods of emergence of adults of Tendipedidae and Culicidae.

#### SCIARIDAE

*Platosciara* sp.—1 ♂ (CNC) (Trap 4: July 24).

*Bradysia jucunda* (Joh.).—1 ♂ (CNC) (Trap 1: June 15).

*Bradysia* sp.—1 ♀ (Trap 3: July 7).

#### STRATIOMYIDAE

*Odontomyia virgo* Wied.—1 ♀ (Trap 4: July 3). James (1936) presents numerous records of this species from Ontario.

*Microchysa polita* (L.).—1 ♂ (Trap 1: June 1). James (1935) includes records of this species from Ontario.

#### RHAGIONIDAE

*Hilarimorpha* sp.—1 ♂ (CNC) (Trap 1: June 10). Greene (1926) discusses the habits of larvae, not including *Hilarimorpha*, in this family and reports that some live in water and are predacious.

#### EMPIDAE

*Platypalpus aequalis* Lw.—1 fly (Trap 1: June 14). Curran (1934) records that immature stages of insects in this family are not well known but that some larvae dwell in streams.

#### DOLICHOPODIDAE

*Dolichopus albicoxa* Aldr.—2 ♂ ♂ (Trap 2: June 11, 29).

*Dolichopus eudactylus* Lw.—1 ♀ (Trap 3: July 1). Loew (1864) records this species from New York and Massachusetts.

*Dolichopus detersus* Lw.—1 ♂ (Trap 4: August 4). VanDuzee *et al.* (1921) record this species from near Toronto and Montreal. It was trapped at Hamilton by Judd (1953).

*Dolichopus ovatus* Lw.—1 ♂ (Trap 4: June 8). Loew (1864) records this species from North America.

*Dolichopus alacer* V.D.—1 ♂ (Trap 2: July 12).

*Dolichopus gratus* Lw.—1 fly (Trap 1: June 27). Loew (1864) records this species from New York.

*Argyra robusta* Johnson.—1 ♀ (Trap 3: June 22). This species was redescribed from specimens collected at the type locality in Quebec by VanDuzee (1925).

*Pelastoneurus vagans* Lw.—5 ♀♀ (2, CNC) (Trap 3: June 27—1, June 28—1, June 29—1; Trap 4: July 8—1, August 2—1). This species was trapped at Hamilton (Judd, 1953) and is distributed elsewhere in eastern North America (Loew, 1864; Van-Duzee, 1923).

*Rhapium* sp.—1 ♀ (CNC) (Trap 4: July 6). Curran (1927), in discussing the nearctic species of *Rhapium*, records that several species are found along streams, muddy banks and in swampy areas.

*Campsicnemus hirtipes* Lw.—2 ♂♂, 2 ♀♀ (Trap 1: June 29—1, July 4—1, July 6—1; Trap 4: July 4—1). Curran (1934) records that *Campsicnemus* occurs on the surface of small pools and Loew (1864) records *C. hirtipes* from Pennsylvania.

*Gymnopternus nigribarbus* Lw.—1 ♀ (Trap 2: June 13). Loew (1864) records this species from Pennsylvania.

*Gymnopternus barbatulus* Lw.—1 ♂ (Trap 1: July 16). Loew (1864) records this species from the "Middle States."

#### CHLOROPIDAE

*Lasiopleura shewelli* Sabr.—1 ♀ (Trap 1: July 14). Sabrosky (1951) records this species from localities in Ontario, including the Dundas Marsh, Hamilton, where the holotype was collected.

*Lasiopleura hirtoides* Sabr.—1 ♀ (CNC) (Trap 3: June 12). Sabrosky (1951) records this species from Michigan.

#### EPHYDRIDAE

*Scatella picea* Wlk.—13 flies (Trap 2: June 7 to July 5—9; Trap 3: July 1—1; Trap 4: July 6—1; Trap 5: May 30—1, May 31—1). Most of these insects emerged in Trap 2 (table 1). *S. picea* was trapped at Hamilton (Judd, 1953).

*Scatella (tenuicosta* Coll.?).—4 flies (Trap 2: June 10—1, June 16—1, June 19—1, July 6—1).

*Notiphila olivacea* Cress.—1 fly (Trap 2: July 1). This species was trapped at Hamilton (Judd, 1953). Berg (1950a) reports finding larvae of *Notiphila* attached to roots of *Potamogeton*.

*Dichaeta caudata* (Fln.).—4 flies (Trap 4: June 25—1, July 7—1, July 14—1, July 20—1). These flies were caught in Trap 4 while it was still afloat. This species has been collected at Hamilton (Judd, 1953).

*Ochthera mantis* (Deg.).—1 fly (Trap 4: July 26). Usinger *et al.* (1956) record that adults are common along marshy stream margins.

*Parydra bituberculata* Lw.—1 fly (Trap 1: October 4). Loew (1862) records this species from the "Middle States."

*Parydra quadrubituberculata* Lw.—2 flies (Trap 1: May 22; Trap 4: September 8). Loew (1862) records this species from the "Middle States."

*Hydrellia griseola* (Fln.).—1 fly (Trap 3: July 8). This species was trapped at Hamilton by Judd (1953).

*Discocerina obscurella* (Fln.).—2 flies (Trap 1: June 18; Trap 2: June 17). This species was collected at Hamilton (Judd, 1949a).

#### BOBORIDAE

*Leptocera michigana* Sabr.—4 flies (Trap 2: June 15—1; Trap 5: June 5—1, June 8—1, June 28—1). Curran (1934) records that flies of this family occur in swampy places. Judd (1949a) collected *Leptocera* by sweeping aquatic vegetation in the Dundas Marsh.

*Leptocera limosa* (Lw.).—1 fly (Trap 2: June 30).

*Leptocera fontinalis* (Fln.).—1 fly (Trap 2: June 30).

*Leptocera crassimana* (Hal.).—1 fly (Trap 1: April 24).

*Leptocera* sp.—1 fly (Trap 4: September 10).

## TETANOCERIDAE

*Sepedon fuscipennis* Lw.—1 ♂ (Trap 4: May 21). This species was trapped at Hamilton (Judd, 1953). Berg (1953) records that its larva is predacious on aquatic snails.

*Hedroneura rufa* (Panz.).—1 ♀ (Trap 2: September 29). Berg (1953) records that the larva of this fly is predacious on aquatic snails.

## MUSCIDAE

*Scatophaga furcata* (Say).—1 fly (Trap 1: May 2).

*Limnophora narona* (Walk.).—1 ♀ (Trap 4: July 15).

*Lispe albitarsus* Stn.—1 ♀ (Trap 4: July 26). This species was trapped at Hamilton by Judd (1953).

*Lispe sociabilis* Lw.—7 flies (3, CNC) (Trap 3: July 9—1, August 2—1, August 5—1, August 23—1, September 1—1, October 1—1, October 11—1).

## SARCOPHAGIDAE

*Sarcotachinella sinuata* (Mg.).—1 fly (Trap 5: July 28). This fly emerged in Trap 5 when the depth of the water was about 1 foot. Thompson (1951) records this species as a parasite of grasshoppers. Berg (1953) records that some sarcophagid larvae are predacious on aquatic snails.

## TACHINIDAE

*Wagneria vernata* West.—1 fly (Trap 1: June 9). This fly emerged in the trap when the depth of the water was 11 inches. Thompson (1951) records that flies of the genus *Wagneria*, including *W. vernata*, are parasites of caterpillars of the family Phalaenidae. Usinger *et al.* (1956) record that one species of tachinid fly parasitizes aquatic moths.

## HYMENOPTERA

## BRACONIDAE

*Trioxys* sp. (near *gahani* Smith).—5 wasps (2, CNC) (Trap 1: June 10, 14, 17, 18—4; Trap 3: May 22—1). Muesebeck *et al.* (1951) record that wasps of the genus *Trioxys* are parasites of aphids. No aphids were collected from the traps in which these wasps were found but possibly aphids did crawl through the screening of the trap and the wasps emerged from them. The only plants on which aphids might have been dwelling were scanty fronds of *Lemna minor* which were in traps 1 and 3.

## ICHNEUMONIDAE

*Apsilops?* sp.—1 wasp (CNC) (Trap 3: July 15). One species in this genus, *A. hirtifrons*, is a parasite of the aquatic moth, *Nymphula oblitalis* (Muesebeck *et al.*, 1951). This species was trapped at Hamilton (Judd, 1953).

## SUMMARY

Between March 27 and November 6, 1954, 9,152 adult insects were trapped in five tent-traps set out on five bodies of water tributary to the Thames River at London, Ontario. Most of the insects were species whose larvae are aquatic and whose adults emerge from the water, but a few were insects which commonly dwell on aquatic vegetation at the surface or in the littoral zone. The orders represented were Ephemeroptera (0.1 percent), Odonata (0.1 percent), Trichoptera (0.07 percent), Hemiptera (0.2 percent), Coleoptera (0.2 percent), Diptera (99.27 percent), and Hymenoptera (0.06 percent). Midges of the family Tendipedidae constituted 93.7 percent of the Diptera, and mosquitoes (Culicidae) 5.3 percent of the Diptera. Other families of Diptera represented were Tipulidae, Heleidae, Sciaridae, Stratiomyidae, Rhagionidae, Empidae, Dolichopodidae, Chloropidae, Ephydriidae,

TABLE 1.—Numbers of insects collected in traps.

	Trap 1	Trap 2	Trap 3	Trap 4	Trap 5	Total No. of Insects
	No. of Insects	No. of Insects	No. of Insects	No. of Insects	No. of Insects	Percent of Total
<b>EPHEMEROPTERA</b>						
Hexageniidae						
<i>Hexagenia afflicta</i>	1	100	0	0	0	0
Baetidae						
<i>Calibaetis fluctuans</i>	0	0	0	9	0	0
<b>ODONATA</b>						
Coenagrionidae						
<i>Ischnura verticalis</i>	0	0	0	2	8	80
Aeschnidae						
<i>Anax junius</i>	0	0	0	1	0	0
<b>TRICHOPTERA</b>						
Hydroptilidae						
<i>Hydropsila perditia</i>	0	0	1	0	0	0
<i>Hydropsila</i> sp.	1	100	0	0	0	0
Hydropsychidae						
<i>Chamaetipsyche</i> sp.	4	100	0	0	0	0
Philopotamidae						
<i>Chimarra obscura</i>	1	100	0	0	0	0
<b>HEMIPTERA</b>						
Saldidae						
<i>Saldula confluenta</i>	2	40	2	40	0	0
<i>Saldula pallipes</i>	0	0	1	20	3	60
<i>Saldula</i> sp.	0	0	3	75	0	0
Mesoveliidae						
<i>Mesovelia mulsanti</i>	0	0	0	0	6	100
<b>COLEOPTERA</b>						
Carabidae						



TABLE 1.—(continued).

<i>Bembidion</i> sp.	0	0	1	6	12	66	4	22	1	6	18
<i>Agonum</i> sp.	0	0	0	0	1	100	0	0	0	0	1
Curculionidae	0	0	1	100	0	0	0	0	0	0	1
<i>Ceutorhynchus septentrionalis</i>	0	0	1	100	0	0	0	0	0	0	1
DIPTERA											
Tipulidae											
<i>Tipula furca</i>	1	100	0	0	0	0	0	0	0	0	1
Erioptera caloptera	0	0	0	0	0	0	1	100	0	0	1
Tendipedidae											
<i>Pentaneura illinoensis</i>	3	49	1	17	1	17	1	17	0	0	6
<i>Pelopia punctipennis</i>	0	0	0	0	304	48	322	50	6	2	632
<i>Clinoctanyus flavicinctus</i>	0	0	0	0	0	0	0	100	0	0	1
<i>Anatopynia dyani</i>	0	0	15	94	0	0	0	0	1	6	16
<i>Procladius culiciformis</i>	9	32	0	0	7	25	12	43	0	0	28
<i>Procladius bellus</i>	4	8	0	0	8	16	37	76	0	0	49
<i>Orholodius</i> sp.	0	0	0	0	0	0	0	0	1	100	1
<i>Hydrobaenus</i> sp.	14	12	29	24	10	8	62	52	4	4	119
<i>Cricotopus trifasciatus</i>	9	11	0	0	59	72	13	17	0	0	81
<i>Cricotopus bicinctus</i>	4	1	6	2	246	91	16	6	0	0	272
<i>Polypedium fallax</i>	18	75	1	4	2	8	3	13	0	0	24
<i>Tanytarsus nigricans</i>	3	3	0	0	24	23	75	74	0	0	102
<i>Tendipes decorus</i>	71	49	235	15	221	14	1,047	66	2	0.1	1,576
<i>Tendipes dux</i>	1	4	21	81	0	0	4	15	0	0	26
<i>Tendipes plumosus</i>	0	0	0	0	1	100	0	0	0	0	1
<i>Glyptotendipes lobiferus</i>	20	1	2	0.1	4,256	96	126	2.8	2	0.1	4,406
<i>Glyptotendipes brachialis</i>	0	0	0	0	165	94	10	6	0	0	175
Miscellaneous Tendipedidae	44	5	8	1	234	24	689	70	0	0	975
Heleidae	4	18	1	4	7	32	10	46	0	0	22
Culicidae											
<i>Chaoborus punctipennis</i>	1	1	0	0	136	93	10	6	0	0	147
<i>Chaoborus flavicans</i>	0	0	60	100	0	0	0	0	0	0	60
<i>Anopheles punctipennis</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Culex territans</i>	1	50	1	50	0	0	0	0	0	0	2
<i>Culex pipiens</i>	0	0	269	100	0	0	0	0	0	0	269

TABLE 1.—(continued).

	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5		Total No. of Insects
	No. of Insects	Percent of Total	No. of Insects	Percent of Total	No. of Insects	Percent of Total	No. of Insects	Percent of Total	No. of Insects	Percent of Total	
<i>Culex restuans</i>	0	0	5	100	0	0	0	0	0	0	5
Sciaridae											
<i>Platysticta</i> sp.	0	0	0	0	0	0	1	100	0	0	1
<i>Bradyia jucunda</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Bradyia</i> sp.	0	0	0	0	1	100	0	0	0	0	1
Stratiomyidae											
<i>Odonomyia virgo</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Microchysia polia</i>	1	100	0	0	0	0	0	0	0	0	1
Rhagionidae											
<i>Hilarimorpha</i> sp.	1	100	0	0	0	0	0	0	0	0	1
Empididae											
<i>Platypatus aequalis</i>	1	100	0	0	0	0	0	0	0	0	1
Dolichopodidae											
<i>Dolichopus albicoxa</i>	0	0	2	100	0	0	0	0	0	0	2
<i>Dolichopus eudactylus</i>	0	0	0	0	1	100	0	0	0	0	1
<i>Dolichopus deterius</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Dolichopus ovatus</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Dolichopus alacer</i>	0	0	1	100	0	0	0	0	0	0	1
<i>Dolichopus gratus</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Argyra robusta</i>	0	0	0	0	1	100	0	0	0	0	1
<i>Pelationeurus vagans</i>	0	0	0	0	3	60	2	40	0	0	5
<i>Rhaphium</i> sp.	0	0	0	0	0	0	1	100	0	0	1
<i>Campicnemus hirtipes</i>	3	75	0	0	0	0	1	25	0	0	4
<i>Gymnopternus nigribarbus</i>	0	0	1	100	0	0	0	0	0	0	1
<i>Gymnopternus barbatulus</i>	1	100	0	0	0	0	0	0	0	0	1
Chloropidae											
<i>Lasioptera shewelli</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Lasioptera hirtoides</i>	0	0	0	0	1	100	0	0	0	0	1

TABLE 1.—(continued).

	0	0	9	69	1	8	1	8	2	15	13
Ephydriidae											
<i>Scutella picea</i>	0	0	4	100	0	0	0	0	0	0	13
<i>Scutella (tenuicosta?)</i>	0	0	1	100	0	0	0	0	0	0	4
<i>Notiphila olivacea</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Dichaeta caudata</i>	0	0	0	0	0	0	4	100	0	0	4
<i>Ochthera mantis</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Parydra bituberculata</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Parydra quadratuberculata</i>	1	50	0	0	0	0	1	50	0	0	2
<i>Hydrellia griscola</i>	0	0	0	0	1	100	0	0	0	0	1
<i>Disococerna obscurella</i>	1	50	1	50	0	0	0	0	0	0	2
Borboridae											
<i>Lepiocera michigana</i>	0	0	1	25	0	0	0	0	3	75	4
<i>Lepiocera limosa</i>	0	0	1	100	0	0	0	0	0	0	1
<i>Lepiocera fontinalis</i>	0	0	1	100	0	0	0	0	0	0	1
<i>Lepiocera crassimana</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Lepiocera</i> sp.	0	0	0	0	0	0	1	0	0	0	1
Tetanoceridae											
<i>Sepedon fuscipennis</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Hedrona rufa</i>	0	0	1	100	0	0	0	0	0	0	1
Muscidae											
<i>Scatophaga furcata</i>	1	100	0	0	0	0	0	0	0	0	1
<i>Limnophora narona</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Liipe albilaris</i>	0	0	0	0	0	0	1	100	0	0	1
<i>Liipe sociabilis</i>	0	0	0	0	7	100	0	0	0	0	7
Sarcophagidae											
<i>Sarcotachinella sinuata</i>	0	0	0	0	0	0	0	0	1	100	1
Tachinidae											
<i>Wagneria vernalis</i>	1	100	0	0	0	0	0	0	0	0	1
HYMENOPTERA											
Braconidae											
<i>Trioxys</i> sp.	4	80	0	0	1	20	0	0	0	0	5
Ichneumonidae											
<i>Apilops</i> ? sp.	0	0	0	0	1	100	0	0	0	0	1
TOTALS	237	2.7	684	7.5	5,717	62.4	2,483	27.1	31	0.3	9,152

TABLE 2.—Number of insects of the seven orders collected in the traps

[illegible]

Borboridae, Tetanoceridae, Muscidae, Sarcophagidae and Tachinidae. The families of Hymenoptera were Braconidae and Ichneumonidae. The numbers and seasonal occurrence, including the times of maximum abundance, were recorded for each species.

## REFERENCES

- BERG, C. O. 1950—Biology of certain Chironomidae reared from *Potamogeton*. Ecol. Monogr. 20:83-101.
- 1950a—*Hydrellia* (Ephydriidae) and some other acalyptrate Diptera reared from *Potamogeton*. Ann. Entomol. Soc. Amer. 43:375-398.
- 1953—Sciomyzid larvae (Diptera) that feed on snails. J. Parasit. 39:630-636.
- BLATCHLEY, W. S. AND C. W. LENG 1916—Rhynchophora or weevils of northeastern America. Nature Publ. Co., Indianapolis.
- BOHART, R. M. 1948—The subgenus *Neoculex* in America north of Mexico (Diptera, Culicidae). Ann. Entomol. Soc. Amer. 41:330-345.
- BURKS, B. D. 1953—The mayflies, or Ephemeroptera, of Illinois. Bull. Illinois Nat. Hist. Surv. 26:1-216.
- CARPENTER, S. J. AND W. J. LACASSE 1955—Mosquitoes of North America (north of Mexico). Univ. Calif. Press, Berkeley and Los Angeles.
- CURRAN, C. H. 1927—The nearctic species of the genus *Rhaphium* Meigen (Dolichopodidae, Dipt.). Trans. Roy. Can. Inst. 16(1):99-179.
- 1934—The families and genera of North American Diptera. Ballou Press, New York.
- GREENE, C. T. 1926—Descriptions of larvae and pupae of two-winged flies belonging to the family Leptidae. Proc. U. S. N. M. 70 (Article 2).
- HOFFMAN, C. H. 1932—The biology of three North American species of *Mesovelia* Hemiptera-Mesoveliidae). Can. Entomol. 64:88-95, 113-120, 126-134.
- HOWARD, L. O., H. G. DYAR AND F. KNAB 1912—The mosquitoes of North and Central America and the West Indies. Carnegie Inst. Washington, Publ. 159, vol. 1. Lord Baltimore Press, Baltimore.
- JAMES, M. T. 1935—A review of the nearctic Geosarginae (Diptera, Stratiomyidae). Can. Entomol. 67:267-275.
- 1936—The genus *Odontomyia* in America north of Mexico (Diptera, Stratiomyidae). Ann. Entomol. Soc. Amer. 29:517-550.
- JOHANNSSEN, O. A. 1905—Aquatic nematoceros Diptera. II. New York State Mus. Bull. 86:76-315.
- JUDD, W. W. 1949—Insects collected in the Dundas Marsh, Hamilton, Ontario, 1946-47, with observations on their periods of emergence. Can. Entomol. 81:1-10.
- 1949a—Insects collected in the Dundas Marsh, Hamilton, Ontario, 1947-48. J. New York Entomol. Soc. 87:225-231.
- 1953—A study of the population of insects emerging as adults from the Dundas Marsh, Hamilton, Ontario, during 1948. Amer. Midl. Nat. 49:801-824.
- 1954—Results of a survey of mosquitoes conducted at London, Ontario, in 1952 with observations on the biology of the species collected. Can. Entomol. 86:101-108.
- 1956—Results of a survey of calyptrate flies of medical importance conducted at London, Ontario, during 1953. Amer. Midl. Nat. 56:368-405.
- LEONARD, M. D. 1926—A list of the insects of New York. Cornell Univ., Agric. Exp. Stn., Memoir 101.
- LINDROTH, C. H. 1954—Random notes on North American Carabidae (Coleopt.). Bull. Mus. Comp. Zool. (Harvard College) 3:117-161.
- 1955—A revision of the North American species of *Europhilus*, a subgenus of *Agonum* with a note on *Agonum bellfroi* (Coleoptera : Carabidae). Pan-Pacific Entomol. 31:1-14.



- LOEW, H. 1862—Monographs of the Diptera of North America. Part I. Smithsonian Miscell. Coll., 6 (Article 1).
- 1864—Monographs of the Diptera of North America. Part II. Smithsonian Miscell. Coll., No. 171.
- MATHESON, R. 1944—Handbook of the mosquitoes of North America. Comstock Publ. Co., Ithaca, New York.
- MCGAHA, Y. T. 1952—Limnological relations of insects to certain aquatic flowering plants. Trans. Amer. Micros. Soc. 71:355-382.
- MILLER, R. B. 1941—A contribution to the ecology of the Chironomidae of Costello Lake, Algonquin Park, Ontario. Univ. Toronto Studies, Biol. Series, 49 (Publ. Ontario Fish. Res. Lab., 60).
- MUESEBECK, C. F. W., K. V. KROMBEIN, H. K. TOWNES ET AL. 1951—Hymenoptera of America north of Mexico. —Synoptic catalog. U.S. Dept. Agric., Agric. Monogr., No. 2.
- NEEDHAM, J. G., J. R. TRAVER AND Y. HSU 1935—The biology of mayflies. Comstock Publ. Co., Ithaca.
- ROSS, H. H. 1944—The caddis flies, or Trichoptera, of Illinois. Bull. Illinois Nat. Hist. Surv. 23 (Article 1).
- SABROSKY, C. W. 1951—A review of the nearctic species of *Lasiopleura* (Diptera, Chloropidae). Can. Entomol. 83:336-343.
- THOMPSON, W. R. 1951—A catalogue of the parasites and predators of insect pests. Section 2. Host parasite catalogue. Part I. Hosts of the Coleoptera and Diptera. Commonwealth Inst. Biol. Control, Ottawa.
- TOWNES, H. K. 1945—The nearctic species of Tendipedini (Diptera, Tendipedidae (= Chironomidae)). Amer. Midl. Nat. 34:1-206.
- USINGER, R. L., I. LARIVERS, H. P. CHANDLER AND W. W. WIRTH 1952—Biology of aquatic and littoral insects. Univ. Calif. Syllabus Series, Syllabus SS. Univ. Calif. Press, Berkeley.
- , ———, AND ———1956—Aquatic insects of California with keys to North American genera and California species. Univ. Calif. Press, Berkeley and Los Angeles.
- VANDUZEE, M. C. 1923—The *Pelastoneurus* of North America (Dolichopodidae, Diptera). Ann. Entomol. Soc. Amer. 16:30-49.
- 1925—A revision of the North American species of the genus *Argyra* Macquart, two-winged flies of the family Dolichopodidae. Proc. U.S.N.M. 66 (Article 23).
- , F. R. COLE AND J. M. ALDRICH 1921—The dipterous genus *Dolichopus* Latreille in North America. Bull. U.S.N.M. 116.
- WALKER, E. M. 1953—The Odonata of Canada and Alaska. Vol. I. The Zygoptera—damselflies. Univ. Toronto Press, Toronto.

## Microbial Population in the Rhizosphere of Yellow Poplar Seedlings<sup>1</sup>

R. D. Shipman

*Santee Research Center, Southeastern Forest Experiment Station,  
Charleston, S. C.*

Living and dead microorganisms such as fungi, bacteria, and actinomycetes exert a profound influence upon the genetical development of soil profiles. Indirectly, through physical, chemical and microbiological decomposition, they may also affect the growth of forest trees. Although the quantity, or numerical content of organisms in any given soil are only relative indices of forest soil fertility, they offer valuable clues to potential plant growth and other site factors. Lohnis and Fred (1923) concluded that a determination of bacterial numbers in the soil is worthless as an attempt in interpreting soil phenomena. Later investigators, Waksman (1927) and Waksman and Starkey (1931) have clearly shown that numerical counts are important as well as indicative, when used in conjunction with other edaphic and climatic factors. Shipman (1947), on studies of soil organisms in both natural and planted forests, has demonstrated that forest site quality is indirectly related to soil organism populations. An intimate relationship was found between the number of microbes in the surface layers and age of the site.

While the qualitative distribution of soil microorganisms remains much the same, there are very marked differences in the quantitative relationships of any given soil, as shown by Waksman and Starkey (1931). Considerable work has been done concerning the abundance of microorganisms in the root zone of cultivated plants. Hiltner (1904) introduced the term "rhizosphere" to designate that portion of the soil which is influenced by the immediate plant root system, or soil adjacent or adhering to the roots. He found, as have others, Hoffman (1915), Rakitzkaia (1926), Smith (1928) and Starkey (1929), that the rhizosphere soil supported greater microbial activity than soil more distant from the roots. It has been shown by Smith (1928) that the maximum effect or activity of organisms on the roots of leguminous plants occurs in an advanced stage of seedling development, particularly in the flowering stage. Others have presented evidence that different plants exert varying influences on the activity of soil organisms. However, there is practically no information concerning the influence of higher plants, such as forest tree seedlings, on soil microorganisms in the seedling stage of plant development.

The present study was carried out to investigate the quantitative distribution of certain classes of soil organisms which may be present on the root system of yellow poplar (*Liriodendron tulipifera* L.) seedlings. The objectives were 1) development of a technique whereby soil organisms can be simultaneously isolated from both the rhizosphere and soil distant from the

<sup>1</sup> The author acknowledges the administrative assistance offered by Dr. T. D. Stevens, Head Dept. of Forestry, Michigan State University, East Lansing, Michigan.

rhizosphere, and 2) to determine by the plate count method, the quantities of fungi, bacteria and actinomycetes which occur at four different stages of seedling vegetative development.

### MATERIALS AND METHODS

#### SOIL SAMPLING AREA

Two distinct soil types, or sampling areas, were selected from an immature stand of yellow poplar located in Cass County, Michigan. In each of these soil types, one a sandy loam and the other a loam to sandy loam, nine soil blocks (20" x 15" x 6") were taken at random. The blocks were lifted *in situ* from the area by means of a cutting blade and transported to the greenhouse. These blocks were then placed in greenhouse benches and arranged as a randomized unit. After the individual blocks had stabilized, pertinent chemical and edaphic data were obtained for each soil type as shown in table 1. An analysis of variance computation showed that no significant variation existed between soil types. Consequently, the soils were considered as a composite with similar soil characteristics.

#### GREENHOUSE PROCEDURE

In December 1951, one-year old yellow poplar seedlings were lifted prematurely from nursery beds. The seedlings were taken to the greenhouse, roots were washed free of adhering soil with distilled water, and 54 seedlings were transplanted at a 4 x 6 inch spacing in each soil type. Controlled laboratory conditions of air temperature and relative humidity were maintained throughout the experiment. At periodic intervals, equal amounts of water were added to the seedlings. The first indication of leaf emergence occurred on January 7, 1952, approximately one month after transplanting. The stem length in centimeters and fresh weight in grams was obtained initially, and again after the expiration of the test. In order to eliminate the possibility of variation in growth and fresh weight of material produced by the two soil types, an analysis of variance was again computed. No significant difference in height growth or fresh weight was found (table 2).

TABLE 1.—Chemical and physical characteristics obtained on two soil types from which organisms were isolated

Soil Type	Fine clay	Sand	Silt plus clay	Soil pH	Soil Moisture Percent	Organic Matter Percent	Nitrogen Percent	C/N Ratio	Total porosity Percent
Sample 1									
Sandy loam (acid variant)	13.2	61.5	38.5	5.4	15.3	2.03	.119	20:1	46.8
Sample 2									
Loam to sandy loam acid variant)	15.1	59.2	40.8	5.3	14.5	2.16	.127	19:1	48.9

Sixteen seedlings were selected at random from the soil plots and tagged for soil rhizosphere sampling. All herbaceous vegetation (roots and stem) was carefully removed from the vicinity of the sample seedlings whenever it occurred above ground. This was done in order to reduce possible contamination from roots of other vegetation at the time of the microbial isolation.

#### LABORATORY METHODS

Samples of soil from the rhizosphere and soil distant were obtained simultaneously by means of the soil extractor (fig. 1). The light metal

TABLE 2.—Percentage increase in growth and fresh weight of seedlings produced by each soil

Soil Type <sup>1</sup>			
Sandy loam			
Item	Average length		Average seedling growth Percent
	Dec. 1951 cm	Sept. 1952 cm	
Stem length	12.0	14.6	21.7
Sandy loam to loam			
Item	Average length		Average seedling growth Percent
	Dec. 1951 cm	Sept. 1952 cm	
Stem length	12.8	15.9	24.2
Sandy loam			
Fresh-weight material produced	Fresh wt Dec. 1951 Gms	Fresh wt Sept. 1952 Gms	Average fresh wt increase Percent
	3.1	5.5	
Sandy loam to loam			
Fresh-weight material produced	Fresh wt Dec. 1951 Gms	Fresh wt Sept. 1952 Gms	Average fresh wt increase Percent
	3.3	5.9	

<sup>1</sup> Basis: 54 seedlings per soil type.

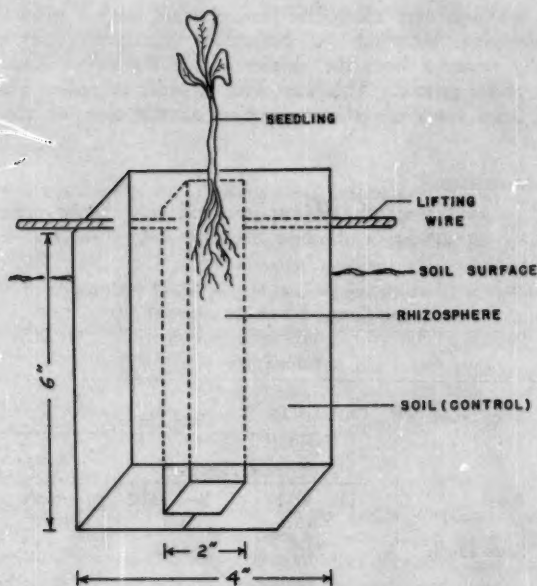


Fig. 1.—Diagram of soil extractor with seedling in place. The inner sleeve removes soil from the rhizosphere and the outer sleeve removes soil distant from the root zone (control). The complete extractor is placed over the seedling and the soil is lifted *in situ* by means of the lifting wire.

device was first dipped in alcohol and ignited in order to eliminate contamination. By carefully placing the extractor over the seedling and pressing down to a depth of 6 inches, blocks of soil containing both rhizosphere and distant soil were removed by means of the lifting wire. Four seedlings were sampled at various stages of seedling development: (1) dormant bud (2) breaking bud (3) primary leaf and (4) secondary leaf. These phenological stages and their corresponding number of leaves and amount of leaf surface produced are shown in fig. 2.

The cultural procedure for obtaining counts on the rhizosphere soil is described by Timonin (1940). First, a soil moisture sample was taken on each soil sample so that necessary corrections for moisture could be made. Soil acidity was determined by the glass-electrode pH meter. The blocks of soil containing the seedling roots were placed (separately from the control soil) on sterile petri dishes. This soil was then gently crushed with as little tearing of the roots as possible, and the roots removed by shaking. Seedling roots were then severed from the stem. The remaining roots with the small amount of soil attached were then deposited in a sterile flask and weighed. Flask and contents were weighed again and the weight of soil plus attached roots was determined. Assuming the weight of attached soil is



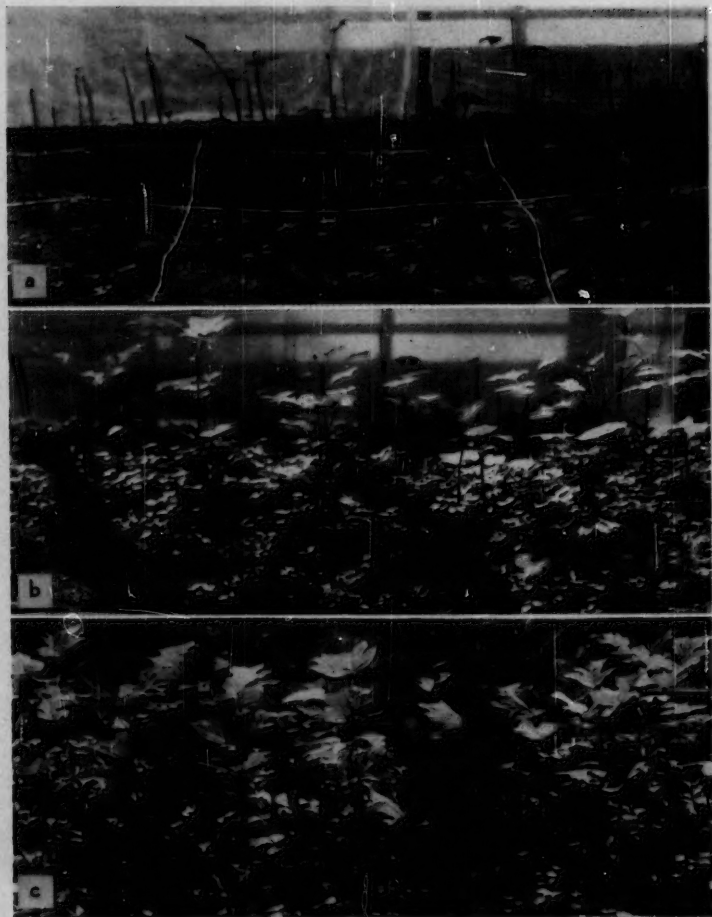


Fig. 2.—Yellow poplar seedlings representing three stages of development. (A) February 1952. Avg. no. leaves 1.8; average leaf diameter 0.5 inches. (B) March 1952. Avg. no. leaves 3.0; average leaf diameter 1.2 inches. (C) April 1952. Avg. no. leaves 4.5; average leaf diameter 2.0 inches.

approximately one-half to one-third of the total weight, dilutions for plating out the organisms were prepared accordingly. Depending on the weight of the attached soil, and after shaking for 5 minutes, a dilution of 1:100 was prepared from the original flask. Further dilutions 1:1000 and 1:10,000 were made using sterile pipettes and shaking each for 1 minute. After the required dilutions were prepared, roots were removed with sterile forceps,

the water evaporated and the soil residue dried to a constant weight at 105°C. The moisture-free rhizosphere soil is obtained in order to compute the necessary dilution coefficients. Similarly, counts were made on the controls, or soil taken from the outer sleeve of the soil extractor.

From the above dilutions, 1 ml of each was dispensed by sterile pipettes into a selective medium and poured aseptically into sterilized petri dishes and subsequently incubated at 28°C. For the fungi, a Peptone Glucose Acid Agar was utilized<sup>2</sup> and for bacteria and actinomycetes, Nutrose Agar was used as a medium<sup>3</sup>. Recent improvements in the plate count method indicate that more precise media are desirable. Waksman's (1927) sodium albuminate agar has been extensively used for bacteria and actinomycetes for similar types of study.

The number of organisms was computed from the average values obtained for the 1:100, 1:1000 and 1:10,000 dilutions. Duplicate plates were run for rhizosphere and control soils which included thirty-two individual soil samples. After the organisms appeared on the plates they were counted by means of a microscope and counting plate and expressed as the number present per gram dry weight of soil:

$$\text{No. colonies per gram dry weight} = \frac{\text{Avg. no. colonies} \times \text{dilution} \times 100}{100 - \text{soil moisture content}}$$

Based upon the arithmetic mean values of the plate counts, the conventional "t" test was applied to determine the significance of the results. Statistical comparisons were made between counts taken from rhizosphere and control soil, and between stages of seedling development.

## RESULTS

### TOTAL ABUNDANCE OF ORGANISMS

Bacteria, as a class of organisms, were present in far greater numbers per gram of moisture free soil than either filamentous fungi or actinomycetes. The total average number of bacteria found was 4,134,220 per gram of soil. Actinomycetes, with 37,937, was closely followed by the fungi with 36,701. These are relative numbers and represent the averages taken at four stages of seedling development. In the rhizosphere, the bacterial population was approximately 138 times greater than either the actinomycete or fungus population. For the control soil (distant from the rhizosphere) the bacterial numbers were 42 times greater than the other two classes of organisms. Thus, it appears that bacteria, at least in numerical terms, showed the greatest total potential activity in the rhizosphere or root zone of yellow poplar seedlings grown on the soil types described.

<sup>2</sup> Agar,  $\text{KH}_2\text{PO}_4$ ,  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , Peptone, Glucose, Distilled water. Reaction pH 5.0-5.4.

<sup>3</sup> Agar, Nutrose, Glucose,  $\text{K}_2\text{HPO}_4$ ,  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ,  $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ , Tap water. Reaction pH 5.8.

#### DENSITY OF ORGANISMS IN THE RHIZOSPHERE

From the data presented in table 3, it is indicated that the average numbers of bacteria and actinomycetes are significantly greater in the rhizosphere than elsewhere (controls). Counts of bacteria and actinomycetes are from 1 to 19 times greater than in the control soil. The only exception occurred in the secondary leaf stage of development, where there was no real difference between the control and rhizosphere counts.

With the fungi, however, this difference is less striking where the controls showed from 0.46 to 0.89 times greater numbers than in the rhizosphere. This difference was statistically significant at the secondary leaf stage of vegetative development.

#### STAGE OF SEEDLING DEVELOPMENT

A highly consistent quantitative relationship with the phenological stage of seedling development is indicated. For all three classes of organisms, the highest R:S ratios were found in the breaking bud stage of development. The greatest difference during this stage occurred with the bacterial population where the number of organisms in the rhizosphere was nearly 19 times greater than in the soil distant. In general, an increase in counts with advancing development of the seedlings is apparent, with a gradual decline in numbers as maturity approaches. This was particularly marked with the bacterial population.

#### DISCUSSION

Organism counts taken from the rhizosphere (root zone) of forest tree seedlings appear meaningless unless comparable estimates are derived some distance from the seedling roots. Consequently, the use of a root: seedling relationship (R:S ratio) in evaluating and interpreting the selective action of roots and soil organisms is highly desirable. (Katznelson, Lockhead and Timonin 1948).

Under conditions as described in this investigation, undoubtedly some portion of the microorganisms reported in the rhizosphere may reflect, in part, organisms present on the root system itself. This arises from the fact that where the total weight of soil is only 1/2 to 1/3 of the total weight, dividing by the soil weight may result in artificially high values. Even so, a comparison of counts between roots and root zone appear to be proportionate. To the degree indicated, use of the described soil extractor reduced the contamination from weed and grass roots. Although it was not possible to eliminate all the lesser vegetation from the greenhouse plots without soil disturbance, the use of soil in place appears to have value. It is under such conditions that forest tree seedlings are found in their natural state.

As pointed out by Timonin (1940), numbers of organisms in the root zone are influenced by many factors: stage of growth, moisture content, soil type and reaction, and treatment of the soil. In this test, a rigid control was exercised over differences arising from soil moisture, soil type and acidity, and variations arising from differences in species and age of plant. For these reasons, it is assumed that the counts given are an expression of organism differences attributed to the rhizosphere and soil distant respectively.

TABLE 3.—Numbers of fungi, bacteria, and actinomycetes from the rhizosphere and soil distant

Class of Organism	Sample from	Phenological Stage of Seedling Development							
		Dormant Bud		Breaking Bud		Primary leaf		Secondary leaf	
		Numbers <sup>1</sup>	$\frac{R}{S}$ ratio	Numbers	$\frac{R}{S}$ ratio	Numbers	$\frac{R}{S}$ ratio	Numbers	$\frac{R}{S}$ ratio
Fungi	Rhizosphere	11,405	.66	26,193	.89	15,432	.78	8,634	.46*
	Soil	17,401		29,386		19,651		18,703	
Bacteria	Rhizosphere	2,993,455	5.4**	6,131,402	18.8**	3,335,590	3.6**	1,324,065	1.4
	Soil	549,277		325,912		922,331		954,849	
Actinomycetes	Rhizosphere	26,182	1.6*	39,422	3.1**	16,281	2.3*	18,392	1.2
	Soil	16,371		12,690		6,945		15,467	

<sup>1</sup> Number of organisms per gram dry weight of soil.<sup>2</sup> R Number organisms in rhizosphere

S Number organisms in soil (control).

\*\* Highly significant (1% level of probability).

\* Significant (5% level of probability).

## SUMMARY

A technique for simultaneous isolation of soil organisms from the rhizosphere and soil distant from the root zone of yellow poplar seedlings is described. The soil extracting method was employed to remove soil containing various numbers of bacteria, actinomycetes and fungi associated with one year old forest tree seedlings. Soil samples removed in their natural state were transported to greenhouse benches, where quantitative counts of soil organisms were obtained from seedling roots at four different stages of seedling development. Organisms were isolated and cultured on selective media using the conventional plate count method, and quantitative estimates of soil organism numbers were made.

Comparative estimates of microbial numbers indicated that bacteria, as a class of organisms, gave the highest R:S ratios. This wide difference, between quantities of bacteria and actinomycetes occurring in the rhizosphere in contrast to counts taken distant from the root zone, was most marked during the breaking bud stage of seedling development.

In general, there was an increase in the number of all three classes of organisms investigated, with advancing stage of yellow poplar vegetative development. Results of this study indicate that future research which includes physiological and qualitative investigation of organisms occurring in the rhizosphere of other tree species is desirable.

## REFERENCES

- FRED, E. B. AND S. A. WAKSMAN 1928—Laboratory manual of general microbiology. McGraw-Hill Book Co., Inc. New York.
- HILTNER, L. 1904—Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache. Arb. Deut. Landw. Ges. 98:59-78.
- HOFFMAN, C. 1914-15—A contribution to the subject of the factors concerned in soil productivity. Kans. Univ. Sci. Bul. 9:81-99.
- KATZNELSON, H., A. G. LOCKHEAD, AND M. I. TIMONIN 1948—Soil microorganisms and the rhizosphere. Bot. Rev. 14(9):543-587.
- LOHNIS, F. AND E. B. FRED 1923—Textbook of agricultural bacteriology. McGraw-Hill Book Co., New York.
- RAKITZKA, A. 1926—Aerobic fermentation of cellulose under the influence of the soil microflora in the zone of the plant root system. Izv. Nauch. Melior. Inst. No. 13:168-208.
- SHIPMAN, R. D. 1947—Soil organisms in a natural forest and in a plantation forest. Unpublished MF thesis. Univ. of Michigan, Ann Arbor, Michigan.
- SMITH, N. R. 1928—The identification of *B. radiobacter* and its occurrence in soil. J. Bact. 15:20-21.
- STARKEY, R. L. 1929—Some influences of the development of higher plants upon the microorganisms in the soil. II. Influence of the stage of plant growth upon abundance of organisms. Soil Sci. 27:355-379.
- TIMONIN, M. I. 1940—The interaction of higher plants and soil microorganisms. I. Microbial population of rhizosphere of seedlings of certain cultivated plants. Can. J. Res. 18:307-317.
- AND A. G. LOCKHEAD 1948—Distribution of microorganisms in the rhizosphere of a root system. Trans. Royal Soc. Can. 42 Ser. 3(5):175-181.
- WAKSMAN, S. A. 1927—Principles of soil microbiology. The Williams and Wilkins Co., Baltimore, Maryland.
- AND R. L. STARKEY 1931—The soil and the microbe. John Wiley and Sons, New York.



## Natural and Artificial Hybridization Between *Helianthus Mollis* and *H. Occidentalis*<sup>1</sup>

R. C. Jackson

University of New Mexico, Albuquerque

A. T. Guard

Purdue University, Lafayette, Indiana

The classification of species of *Helianthus* has long been a source of difficulty for amateur and professional botanists alike. Watson (1929), in his contribution toward a monograph of the genus, commented on the tendency of certain species groups to intergrade imperceptibly with one another. Heiser (1947, 1949, 1951) has shown that much of the variation encountered in annual sunflowers is due to interspecific hybridization. In diploid perennial species of *Helianthus* lack of genetic barriers to interspecific hybridization have been demonstrated by Long (1955 a,b) and Jackson (1955, 1956). As a result of recent work in the perennial species several supposedly rare taxa have been shown to be naturally occurring interspecific hybrids or their derivatives.

The first putative hybrids between *H. mollis* Lam. and *H. occidentalis* Riddell were recognized and collected by G. Moore in Laclede Co., Missouri. During a recent study of certain perennial sunflowers, the writers encountered numerous populations of natural hybrids between these two species. Several were selected for analysis and are presented here.

### MATERIALS AND METHODS

Artificial hybrids were obtained by rubbing the heads of parental species together during the time of anthesis of the disc flowers which open over a period of several days. The heads were bagged before anthesis and after pollination in order to insure against pollen contamination from other plants. The F<sub>1</sub> hybrids were grown in the greenhouse in 10-inch pots alongside the parental species. Mass collections of the species and naturally occurring hybrids were taken from several different localities in northern Indiana. Usually 25-50 plants were collected from each population. Representative specimens of the artificial and natural hybrids have been deposited in the herbarium of Indiana University and of Purdue University.

Material for cytological study was collected from naturally occurring hybrids and species and from the artificial hybrids and their parents grown in the greenhouse. Immature heads for chromosomal study were fixed in a

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mixture of two parts absolute ethyl alcohol and one part glacial acetic acid. Fixation was usually for 48 hours at room temperature. Microsporocytes were stained with iron-acetocarmine, and the usable slides were made permanent by the introduction of Venetian turpentine. Pollen was stained with annilin blue in Aman's lactophenol for a period of 24 hours. Pollen grains that stained a uniform deep blue were considered viable while those which did not stain at all or only in spots were counted as non-viable.

#### PARENTAL SPECIES

*Helianthus mollis* and *H. occidentalis* are both well-defined species and differ in a number of diagnostic characters (see table 1). Throughout much of their respective ranges they are sympatric in distribution. In Indiana both species often occupy the same habitat, occurring along railroad right-of-ways, fence-rows, and roadsides. There appear to be no definite ecological barriers separating them although *H. occidentalis* is sometimes found in more xeric habitats. Field observations have shown that the two species flower at the same time with the duration of flowering being somewhat longer in robust plants of *H. mollis*.

TABLE 1.—A morphological comparison of *Helianthus mollis* (p 171), *H. occidentalis* (p 146), and the artificial hybrid between the two.\*

	<i>H. mollis</i>	F <sub>1</sub> hybrid	<i>H. occidentalis</i>
1. Terminal head			
a. base diameter in mm	15-20	(10)-11-13	7-10
b. phyllary length in mm	10-12	11-16	5-7
c. ray flower number	17-22	(13)-14-16	9-13
2. Typical leaf			
a. index	.43-.68	.29-.42	.11-.28
b. length to main lateral veins in cm	0.5-1.3	1.4-4.4	4.5-9.7
c. shape of leaf base	sub-cordate - cordate	cuneate	attenuate
3. Stem pubescence			
	villous ++++	velutinous ++	strigose +

\* Source of the parental species: *H. mollis* (p 171)—collected by H. Iltis in Root-fork, Arkansas; *H. occidentalis* (p 146)—collected by C. B. Fleiser at Camp Douglas, Wisconsin.

## ARTIFICIAL HYBRIDS

Twenty  $F_1$  hybrids between *H. mollis* and *H. occidentalis* were grown to maturity. Morphologically they were mostly intermediate for characters of the two parents. Exceptions to this were in phyllary length, which was equal to *H. mollis*, and in ray flower number and head diameter which was about the same as *H. occidentalis* in two depauperate plants. Internode length of the hybrids was quite variable, overlapping that of *H. occidentalis*. The hybrids exhibited about the same amount of vigor as the parental species when grown beside them in the greenhouse. Flowering of the species and hybrids occurred at about the same time although it was of longer duration in a few of the hybrids. Contrasting characters of the two species and  $F_1$  hybrid are given in table 1, and typical leaf outlines of the three are shown in figs. 8, 9, 10. Two backcross progeny, resulting from a cross to each parent, were obtained. These were mostly intermediate for characters of the  $F_1$  and recurrent parent.

## CYTOLOGICAL OBSERVATIONS

Both parental species are diploid with  $n = 17$  pairs (Geisler, 1931; Heiser and Smith, 1955). Meiosis in plants used for hybridization experiments and in plants of the species from natural populations was normal. In the hybrids between *H. mollis* and *H. occidentalis* a circle or chain of four chromosomes was found in 38 of 47 cells studied at diakinesis (fig. 18). Since these configurations were not found in either of the parents, it can be assumed that an interchange of relatively large size has occurred in one of the species. No other aberrations were observed.

As a measure of pairing in earlier stages of the species and hybrids the mean minimum chiasma frequency at diakinesis was used. Closed bivalents were considered as held together at either end by a single chiasma while open bivalents were treated as held together by a single chiasma. A circle of four chromosomes would constitute four chiasmata while a chain of three chromosomes would have three. Although this is taken as minimum chiasma frequency, it is probably very near the actual number since most of the closed bivalents were in the shape of a circle and the open bivalents were held together at the end. No univalents were observed in either the species or hybrids. Chiasma frequency and per cent stainable pollen of the species and hybrids are given in table 2.

TABLE 2.—Mean minimum chiasma (Xa.) frequency per cell and per cent stainable pollen of the species and hybrid

Species and hybrid	No. cells studied	Xa. frequency		s	% Stainable pollen
		range	$\bar{x}$		
<i>H. mollis</i>	50	20-29	23.8	$\pm 2.3$	97.0
<i>H. occidentalis</i>	50	21-26	27.4	$\pm 1.3$	98.6
<i>H. mollis</i> X <i>occidentalis</i>	47	17-24	20.2	$\pm 2.3$	49.5

## ANALYSIS OF NATURAL HYBRID AND SPECIES POPULATIONS

The variation of morphological characters of the species and hybrids has been shown by combined use of Anderson's (1936, 1946) methods of pictorialized scatter diagrams and of histograms based on a hybrid index. The Hybrid Index Method is a convenient way of showing differences within and between populations. The shortcomings of this method have been dealt with by Baker (1947), Heiser (1949), and Anderson (1949). Use of pictorialized scatter diagrams allow one to note variations of single characters of an individual plant of a population. Characters used for the scatter diagrams are the same employed as a basis of the hybrid index. The characters used for scoring the parental species and hybrids and their index scores are as follows:

<i>H. occidentalis</i>	intermediates	<i>H. mollis</i>
Head diameter in mm 7-10 = 0	11-14 = 1	15-20 = 2
Phyllary length in mm 5-7 = 0	8-9.9 = 1	10-16 = 2
Ray flower number 9-14 = 0	14-16 = 1	17-22 = 2
Leaf index .11-.28 = 0	.29-.42 = 1	.43-.68 = 2
Shape of leaf base attenuate = 0	narrowly cuneate = 1 cuneate = 2	cordate or subcordate = 3
Length to main lateral veins of the leaf from the base in cm 4.5-9.7 = 0	1.4-4.4 = 1	.5-1.3 = 2
Stem pubescence grades + = 1	++ = 2, +++ = 3	++++ = 4

In the several populations of parental species which were sampled, little variation was observed in the characters studied. Histograms and scatter diagrams of the two species from Indiana are shown in fig. 1. The number above the histograms represents the number of plants scored. The index score of the  $F_1$  hybrid is indicated by the position of the blackened square between the histograms of the two parents.

The six populations of hybrids analyzed here were collected from three counties in northern Indiana. Search for hybrid populations was facilitated by the fact that the two species are quite dissimilar morphologically and hybrids between them are easily recognized.

**Collection Number 720.**—(0.3 mi. north of San Pierre, Starke Co.) Only three plants of *H. mollis* were found in the immediate vicinity, and these were growing among the hybrids. *H. occidentalis* was quite abundant, growing along a railroad right-of-way nearby. The habitat of the hybrids and *H. mollis* was an abandoned pasture on a sandy knoll partially overgrown with bushes. Variation was mostly in the direction of *H. occidentalis* although one clone

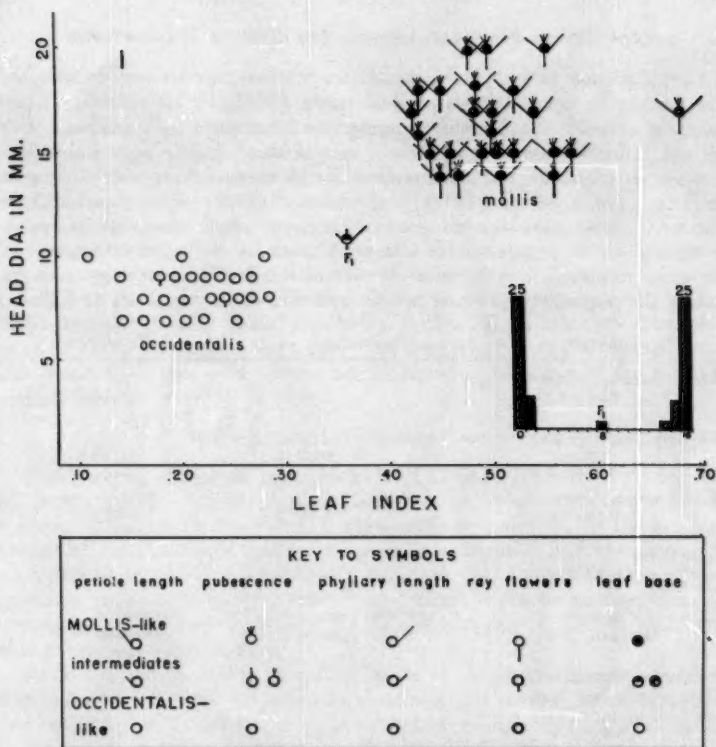


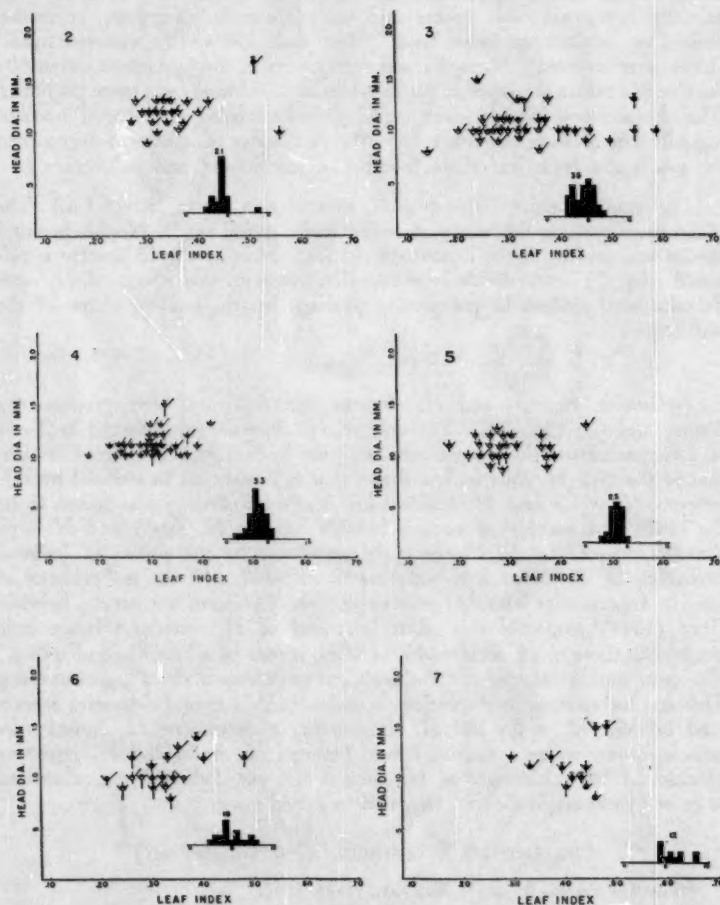
Fig. 1.—Upper part: Pictorialized scatter diagrams and histograms of *H. occidentalis* to the left, *H. mollis* to the right, and between the two the artificial F<sub>1</sub> hybrid. Lower part: Key to the symbols used for the scatter diagrams in figs. 1-7. The term petiole refers to the distance from the leaf base to the two main lateral veins.

was very close to *H. mollis*, differing from this species only in the shape of the leaf base (fig. 2).

**Collection Number 718.**—(3 mi. north of Monon, White Co.) This population (fig. 3) contained a great many individuals with characters intermediate for the two parents. A number of plants showed greater morphological diversity than in any other hybrid population. Variation in leaf index overlapped both species with numerous intermediates. Head diameter was mostly in the range of *H. occidentalis*, a phenomenon observed in other populations. A few of the specimens had a *mollis*-like leaf shape combined with the character of having the leaf mostly basal as in *H. occidentalis*. The habitat was open sandy soil between a railroad right-of-way and a cultivated field. Both species were present in about equal numbers, and the hybrids (approx. 370) constituted about one-third of the local population.



Collection Number 712.—(2.3 mi. southeast of San Pierre, Starke Co.) Over 1,000 flowering individuals were counted in this population. The plants were growing in a narrow band of soil along a fence-row between a gravel road and a cultivated field. The nearest plants of *H. mollis* were some two miles distant, and a population of *H. occidentalis* was found 75 yards from the hybrids. Samples from this population (fig. 4) showed variation mostly in the direction of *H. occidentalis*, probably the result of backcrossing with this species.



Figs. 2-7.—Pictorialized scatter diagrams and histograms of populations of natural hybrids between *H. mollis* and *H. occidentalis*. 2. Population 720; 3. Population 711; 4. Population 712; 5. Population 711; 6. Population 738; 7. Population 730.

*Collection Number 711.*—(Along U. S. highway 421, 1 mi. south of San Pierre, Starke Co.) Over 300 hybrids were growing in a small open area beside a cut-over woodland. The parental species were represented by a minority of plants scattered among the hybrids. Variation was mostly in the direction of *H. occidentalis*, but there was little variation from the average individual of the population (fig. 5).

*Collection Number 738.*—(Southeast corner of Tippecanoe River State Park, Pulaski Co.) The habitat of this population was an abandoned field partially overgrown with bushes and was apparently undergoing succession toward an oak-hickory forest type. More than 350 widely scattered hybrid clones were counted. *H. mollis* was represented in the immediate vicinity by four or five rather depauperate plants while *H. occidentalis* was more abundant. The representative hybrids which were collected exhibited a number of morphologically intermediate characters (fig. 6). A number of specimens approached *H. mollis* closely in leaf shape, number of ray flowers, and pubescence.

*Collection Number 730.*—( $\frac{1}{4}$  mi. west of San Pierre, Starke Co.) The plants were growing between a fence-row and a gravel road. Neither parental species was present in the immediate vicinity. Most of the 12 specimens collected (fig. 7) were decidedly *mollis*-like; however, the effects of *H. occidentalis* were evident in pubescence, phyllary length, and the shape of the leaf base.

#### DISCUSSION

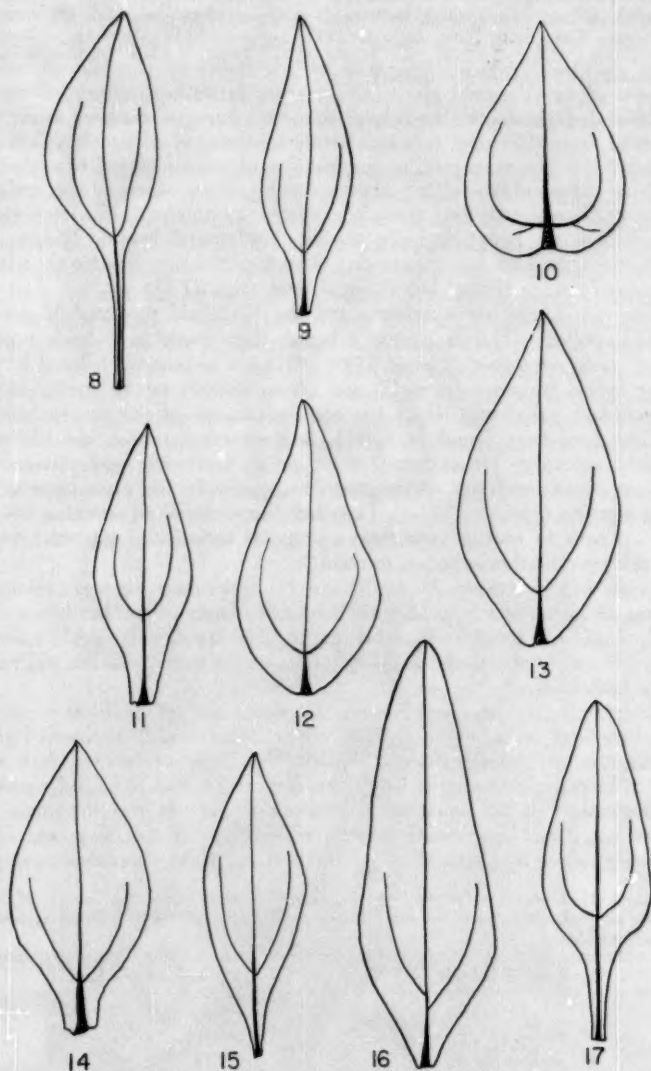
*Helianthus cinereus* and *H. cinereus* var. *Sullivanti* were proposed by Torrey and Gray in 1842. The type of *H. cinereus* was collected in Texas by Drummond and the type of var. *Sullivanti* by Sullivant in Ohio. Examination of the type *H. cinereus* has shown that it is identical to artificial hybrids between *H. mollis* and *H. occidentalis*. Variety *Sullivanti* was found to be the same as a number of natural hybrids between *H. mollis* and *H. occidentalis* collected by G. Moore in Missouri and by the writers in Indiana. Probably var. *Sullivanti* is a backcross to *H. mollis*. From the evidence at hand it appears that both *H. cinereus* and var. *Sullivanti* are natural hybrids. Gray (1884) suspected this when he stated of *H. cinereus*—"heads little larger than those of *H. occidentalis*, of which it may be a hybridized offspring." The same author referred var. *Sullivanti* to synonymy under *H. doronicoides*. This was incorrect since the variety is undoubtedly a hybrid derivative from a cross between *H. mollis* and *H. occidentalis*. Furthermore, *H. doronicoides* is now known to be a natural hybrid between *H. mollis* and *H. giganteus* (Jackson, 1956). Inasmuch as *H. cinereus* and var. *Sullivanti* are considered to be of hybrid origin they are relegated to hybrid status.

#### HELIANTHUS X CINEREUS T. & G. (pro sp.)

*Helianthus cinereus* T. & G. Fl. N.A., 2:324. 1842.

*H. cinereus* var. *Sullivanti* T. & G. Fl. N.A., 2:324. 1842.

*Specimens examined.*—OHIO: Near Columbus, 1840, Sullivant (GH, type of var. *Sullivanti*). INDIANA. CASS CO.: on a sand hill, Sept. 12, 1943, Deam 55460 (IND); WHITE CO.: open, sandy soil, 3 mi. N of Monon, Aug. 22, 1954, Jackson 718-34



Figs. 8-17.—Typical leaves of the two parental species and the artificial and natural hybrids between them. 8. *H. occidentalis*; 9. Artificial hybrid between *H. mollis* and *H. occidentalis*; 10. *H. mollis*; 11-17. Natural hybrids between *H. mollis* and *H. occidentalis*. All ca.  $\times 1/3$ .

(IND); STARKE CO.: 1 mi. S of San Pierre in open area beside cut-over woodland, Aug. 29, 1954, Jackson 711-17 (IND); PULASKI CO.: an abandoned field, SE corner of Tippecanoe River State Park, Aug. 8, 1955, Jackson 730-10 (UNM). MISSOURI. LACLEDE CO.: Sept. 3, 1939, G. Moore (F). TEXAS: Exact location unknown, Drummond (NY, type of *H. cinereus*).

There is little doubt that hybridization and introgression have in the past presented many difficulties to a satisfactory treatment of *Helianthus*. This has been due, for the most part, to the inability or refusal of earlier workers to recognize the possibility of hybridization as a primary source of the variation which produced gradations from one species to another. The two species studied here are morphologically distinct, but natural hybrids bridging the gap between them are not uncommon. This is particularly true for the various leaf types found in natural hybrid populations (figs. 11-17).

The two species are interfertile and the  $F_1$  hybrid produced 50 percent stainable pollen. This is generally higher than found in hybrids between annual sunflower species (Heiser, 1949, 1951). The cause of reduced fertility of the hybrid between *H. mollis* and *H. occidentalis* can be attributed to a chromosomal interchange which has occurred in one of the parents. Translocations have been found in hybrids between other similar and dissimilar perennial species of *Helianthus* (Jackson, 1955; Long, 1955a,b). In hybrids between annual sunflower species they are apparently the main cause of reduced sterility (Heiser, 1947). Thus far, chromosomal repatterning has not been sufficient to exclude gene flow among the annual and perennial species in which hybridization is known to occur.

In the hybrid between *H. mollis* and *H. occidentalis* the mean minimum chiasma frequency was reduced from that of the latter parent, but it was close to *H. mollis* and could overlap this species when standard error is considered (see table 2). Apparently the chromosomes of the two species are still rather highly homologous.

External isolating barriers between *H. mollis* and *H. occidentalis* appear to be very weak or lacking in Indiana. Both species have been observed growing together in extensive stands. Possibly one type of barrier which may serve to keep the species apart is selective fertilization and pollen tube growth. Although there is no experimental evidence to support this hypothesis for *Helianthus*, it has been shown to occur within races of *Zea mays* and *Lycopersicon esculentum* (Jones, 1922). Seed set in hybrid populations was gen-

TABLE 3.—Comparison of seed set in natural populations of *H. mollis*, *H. occidentalis* and hybrids between the two. Based on ten terminal heads selected at random for each population.

Species and hybrids	Seed set per head	
	range	mean
<i>H. mollis</i>	56-106	77.9
<i>H. occidentalis</i>	22-49	36.9
<i>H. mollis</i> x <i>occidentalis</i> (718)	6-39	19.9
<i>H. mollis</i> x <i>occidentalis</i> (712)	19-84	44.1
<i>H. mollis</i> x <i>occidentalis</i> (720)	5-34	17.1
<i>H. mollis</i> x <i>occidentalis</i> (711)	12-30	21.8

erally lower than the species (table 3). This would always give the parental species numerical majority providing they were as vigorous and prolific in vegetative reproduction as the hybrids. However, there is a slight possibility that the hybrids may be better able to withstand disturbed conditions since they are frequently encountered along roadsides and fence-rows in the absence of parents. In one place several hybrids were observed growing in a chicken lot in use at the time.

Clones of hybrids were sometimes encountered in well developed second growth woodlands. In most instances the plants had not attained maximum growth and few were flowering. The presence of hybrids between two heliophytic species in such shaded habitat would seem to indicate that the hybrids were not of recent origin. That only hybrid seed would have been carried to such areas by animals seems highly unlikely. Possibly these hybrids arose sometime after 1900. Previous to this time Starke County was not heavily farmed since most of the fertile soil was in the low wet areas. In 1892 and 1901, drainage ditches were established and thereafter agriculture increased (Grimes, *et al.*, 1917). Most of the woodlands on the higher sand ridges were cut-over, providing new disturbed habitats. The ecological barriers which probably separated *H. mollis* and *H. occidentalis* at that time must have been broken down and permitted hybridization to occur.

The full extent of hybridization between *H. mollis* and *H. occidentalis* is as yet unknown. Hybrids have also been collected in Texas, Missouri, and Ohio, but nothing is known of their frequency in these states.

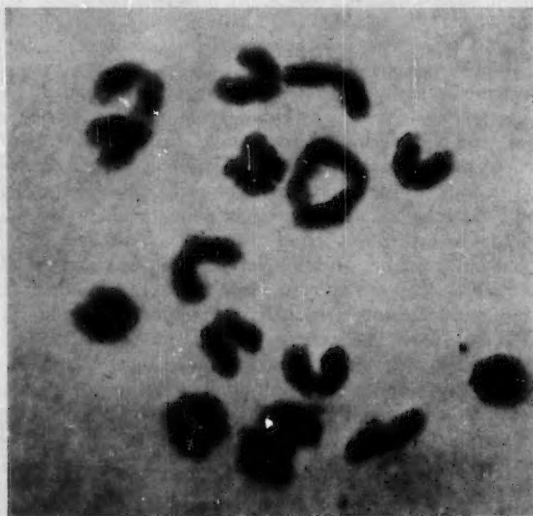


Fig. 18.—Pollen mother cell from  $F_1$  hybrid *Helianthus mollis* X *H. occidentalis* showing a circle of four chromosomes at diakinesis in meiosis I.



In Indiana the effects of introgression between *H. mollis* and *H. occidentalis* are apparently still slight. In the parental populations studied, plants not "fitting" one or the other species were rarely encountered. However, Anderson (1949) has suggested that gene flow between species is of greater biological significance the less apparent it is to casual inspection. This may be true of the two species studied here.

There is a somewhat greater variation of pubescence and leaf base shape in specimens of *H. mollis* from Indiana than is found in plants of the species from other areas. Whether this can be attributed to hybridization with *H. occidentalis* alone is doubtful. *Helianthus mollis* has been found to hybridize naturally with three other perennial species in Indiana (Jackson, 1955). In one small, recently disturbed area, approximately 70 x 35 yards, hybridization of *H. mollis* with *giganteus*, *divaricatus*, and *occidentalis* had occurred. Furthermore, *H. occidentalis* is known to hybridize naturally with two other perennial species in addition to *H. mollis* (Jackson and Guard, 1955). All are found in northern Indiana. Thus any extensive study of variation of the perennial species of *Helianthus* in northern Indiana, and doubtless other areas, is complicated by the fact that variation for a number of characters of a species could not, with certainty, be attributed to introgression from one particular species. For example, an artificial hybrid between *H. mollis* and *H. atrorubens* L. has been successfully crossed to *H. grosseserratus* Martens, and the progeny were 30-50 percent pollen fertile. Although *H. atrorubens* does not occur in Indiana, it nevertheless illustrates the point. It is rather doubtful that our present methods of studying hybridization would be adequate for detecting introgression when more than two species are involved.

#### SUMMARY

*Helianthus mollis* and *H. occidentalis* are, on the basis of morphology, quite dissimilar species. Natural hybrids between the two have been collected in four states, and several hybrid populations from Indiana have been analyzed. The specific and varietal names previously applied to the hybrids have been changed to indicate hybrid status. The artificial hybrid has been grown and analyzed. Morphologically, it is mostly intermediate for characters of the two species. The hybrid was found to produce about 50 per cent stainable pollen. A circle or chain of four chromosomes was usually observed at diakinesis, indicating that the species differ for a chromosomal interchange. The mean minimum chiasma frequency of the hybrid was lower than for *H. occidentalis* but about the same as for *H. mollis*. Analysis of natural hybrid populations has shown that many intermediate types are produced which bridge the gap of morphological differences between the two species. Ecological barriers separating the species in Indiana appear to be weak or lacking. Introgression between *H. mollis* and *H. occidentalis* has probably occurred, but analysis may be complicated by hybridization among several perennial species of *Helianthus* in the same areas.

## REFERENCES

- ANDERSON, E. 1936—Hybridization in American Tradescantias. *Ann. Mo. Bot. Gard.* 23:511-525.
- 1946—Maize in New Mexico; a preliminary survey. *Ibid.* 33:147-247.
- 1949—Introgressive Hybridization. John Wiley & Sons, New York.
- BAKER, H. G. 1947—Criteria of hybridity. *Nature* 159:222-223, 546.
- GEISLER, F. 1931—Chromosome numbers in certain species of *Helianthus*. *Butler Univ. Bot. Studies* 11:53-62.
- GRAY, A. 1884—Synoptical Flora of North America. Vol. 1, part 2.
- GRIMES, E. J., W. BARRET, AND T. M. BUSHNELL 1917—Soil Survey of Starke County, Indiana. U.S. Department of Agriculture.
- HEISER, C. B. 1947—Hybridization between the sunflower species *Helianthus annuus* and *H. petiolaris*. *Evolution* 1:249-262.
- 1949—Study in the evolution of the sunflower species *Helianthus annuus* and *H. Bolanderi*. *Univ. Calif. Publ. Bot.* 23:157-208.
- 1951—Hybridization in the annual sunflowers: *Helianthus annuus* x *H. debilis* var. *cucumerifolius*. *Evolution* 5:42-51.
- AND D. M. SMITH 1955—New chromosome numbers in *Helianthus* and related genera (Compositae). *Proc. Ind. Acad. Sci.* 64:250-253.
- JACKSON, R. C. 1955—Natural hybridization in perennial sunflowers centered about *Helianthus mollis*. Ph.D. Thesis. Purdue Univ.
- 1956—The hybrid origin of *Helianthus doronicoides*. *Rhodora* (in press).
- AND A. T. GUARD 1956—Hybridization of perennial sunflowers in Indiana. *Proc. Ind. Acad. Sci.* (in press).
- JONES, D. F. 1922—Selective fertilization and the rate of pollen tube growth. *Biol. Bull.* 53:167-174.
- LONG, R. W. 1955a—Hybridization in perennial sunflowers. *Amer. J. Bot.* 42:769-777.
- 1955b—Hybridization between the perennial sunflowers *Helianthus salicifolius* A. Dietr. and *H. grosseserratus* Martens. *Amer. Midl. Nat.* 54:61-64.
- TORREY, J. AND A. GRAY 1842—Flora of North America. II.
- WATSON, E. E. 1929—Contributions to a monograph of the genus *Helianthus*. *Papers Michigan Acad. Sci.* 9:305-475.

# Climax Forest Herbs in Prairie

J. Roger Bray<sup>1</sup>

University of Minnesota, Minneapolis

The occurrence of three climax forest herbs, *Claytonia virginica*, *Erythronium albidum* and *Trillium recurvatum*, was noted by Gleason (1912) on a prairie moraine north of Royal in east-central Illinois. Gleason observed that, "These forest mesophytes produce seed in this region so seldom and propagate by vegetative means so regularly, that they cannot be considered recent invaders from the forest upon the prairie." He concluded that these species might be survivors from a forest occupancy which was of greater extent in the post-Glacial past.

As part of an ecologic study of the prairie-forest border, an investigation of the occurrence of forest plants in native prairie was undertaken in an attempt to further document the Gleason observations. Data were gathered from field study, from the literature, and from correspondence with taxonomists and ecologists in the Middle West.

## RESULTS AND DISCUSSION

The results summarized in table 1 are from studies in which three or more herbs were found in prairie that can be considered climax forest species. Nomenclature in tables 1 and 2, and in the text is after Gleason (1952). Not included in the table are observations of *Claytonia virginica* and *Erythronium albidum* by Steyermark (1955) in Missouri prairie; of *Ranunculus septentrionalis* by Fell (1955) in north-central Illinois; of *Claytonia virginica* by Brendel (1887) in the Peoria area of Illinois; and of *Mertensia virginica* by Conard (1956) in Iowa. In addition to the species of the table, *Desmodium glutinosum* and *Rudbeckia laciniata* were noted by Hilgard (1915) and *Osmorhiza claytoni* by the Wisconsin workers.

The four surveys presented in table 1 were made on the periphery of the prairie peninsula as outlined by Transeau (1935). Data in column three is from Curtis, Greene, and Bray (1955) and lists presence in native prairie in Green County in southern Wisconsin. Column four is from presence surveys by Jackson (1956) and Stearns (1956) in the Monon prairie area of west-central Indiana. Column five is from the surveys made in the late 1800's and early 1900's by Mead (in Kibbe, 1952) in Hancock County, Illinois; and column six is from Hilgard on the southern edge of the prairie peninsula in southern Illinois.

The Hilgard manuscript was especially valuable to the study. In the late 1830's and early 1840's, E. W. Hilgard made extensive collections on spring trips through the prairies of St. Claire, Clinton, Marion, and Wayne Counties. A report of his trips, together with a commentary and listing of

<sup>1</sup>The author wishes to thank the men who responded to his questionnaire, and Dr. A. G. Vestal who generously supplied reference to the Hilgard manuscript.

TABLE 1.—Climax forest herbs in prairie

	%PP	%PC	WW	JS	M	H*
<i>Allium tricoccum</i> *	00	100	*		*	
<i>Arisaema triphyllum</i> *	05	90	*			*
<i>Caulophyllum thalictroides</i> *	00	90				*
<i>Claytonia virginica</i> *	00	90		*	*	*
<i>Collinsia verna</i>	—	—				*
<i>Dentaria laciniata</i> *	00	90		*		*
<i>Dicentra cucullaria</i>	00	70		*		*
<i>Erythronium albidum</i> *	00	90				*
<i>Galium concinnum</i>	05	50	*			
<i>Geum canadense</i>	00	70				*
<i>Hydrophyllum virginianum</i> *	00	90	*	*		
<i>Isopyrum bternatum</i>	00	30		*		
<i>Laportea canadensis</i>	00	80		*		*
<i>Mertensia virginica</i>	—	—				*
<i>Mitella diphylla</i> *	00	20		*		
<i>Phlox divaricata</i>	00	50		*		*
<i>Podophyllum peltatum</i>	05	90	*			*
<i>Polemonium reptans</i>	00	50	*	*		*
<i>Ranunculus septentrionalis</i>	00	50	*		*	
<i>Sanguinaria canadensis</i> *	00	100	*	*		*
<i>Trillium recurvatum</i> *	00	70	*	*		*

\* %PP signifies per cent presence in 20 stands of the incipient end of the upland hardwoods continuum of southern Wisconsin. %PC signifies per cent presence in 10 stands of the climax end. WW is Wisconsin workers; M is Mead; JS is the work of Jackson or Stearns; and H is Hilgard. Species names followed by an asterisk are those for which data on life history is available.

forest plants in prairie by Dr. A. G. Vestal, and present-day nomenclature by Dr. R. A. Evers, will be published in a biography of Hilgard by Dr. Hans Jenny.

A few quotations from the Hilgard manuscript will demonstrate the combinations of prairie and forest species which he observed:

The level black prairie was dotted with large islands alternately of hazel, (*Corylus americana*) and of blackberry (*Rubus villosus*) or sometimes the two intermixed. . . . Within these shrubby areas the grass was much suppressed, but *Castilleja coccinea* was abundant as well as *Trillium recurvatum* and *T. viride*, *Erythronium albidum*, *Tradescantia virginica*, *Eryngium aquaticum*; while here and there *Lilium philadelphicum* and *L. canadense* were visible, and very rarely the beautiful *Cypripedium spectabile* . . . while the yellow *C. parviflorum* belonged more to the open ground.

*Penstemon pubescens* also frequently formed dense growths, but more usually was scattered among the low grass, with *Gerardia purpurea*, *Coelestina coerulea*, *Erigeron belidifolium*, *Claytonia virginica*, *Dentaria laciniata*, *Viola cucullata*, *V. pedata*, and *V. sagittata*; *Dielytra cucullaria*, *Sanguinaria canadensis*, *Collinsia verna*, *Leonice thalictroides*, *Podophyllum peltatum*, *Mimulus ringens* and *M. alatus*, *Delphinium azureum*, *D. exaltatum*; . . .

Data on forest herb composition from the Ecology Laboratory of the University of Wisconsin is included in table 1. This data, summarized in columns 1 and 2 of the table, shows the per cent presence of herbs in stands at opposite ends of the upland hardwoods continuum of Curtis and McIntosh (1951). The 20 stands in column 1 are from the 300-600 interval and are dominated by various mixtures of *Quercus macrocarpa*, *Q. velutina*, *Carya ovata*, *Prunus serotina* and other minor species. The 10 stands of column 2

are of the terminal forest end from 2400 to 3000 with *Acer saccharum*, *Tilia americana*, *Carya cordiformis*, and *Ulmus rubra* as important species.

The species chosen for inclusion in table 1 were those which peaked strongly toward the maple-basswood forests and which showed per cent presence of less than 10 in the incipient forest interval. Their absence in pioneer forest increases their value as indicator species since many species of pioneer forest also occur in prairie (Bray, 1955). It is reasonable to assume that the same patterns of forest occurrence will be valid for the herbs of table 1 in the other areas of the Middle West in which they are found. Some of the species in table 1, as will be discussed in a following paragraph, may have broad amplitudes, as perhaps has *Polemonium reptans*, while others, as *Claytonia virginica*, which becomes weedy in southern United States, are adventurers in a part of their range. The species of the table comprise, however, over one-half of the herbs which peak in the climax interval of the upland forest as listed in Gilbert (1953), and their appearance in prairie requires a fuller explanation than that of a chance occurrence.

#### JUDA PRAIRIE SURVEY

A detailed presence study was made of a prairie near Juda in southern Wisconsin, which has an unusually high number of maple-basswood herbs. A list of the species present in Juda prairie is shown in table 2. Additional information on nearby stands from the files of the Wisconsin Ecology Laboratory is summarized in columns 1 through 3 of the table. The first column shows species presence within a maple-basswood forest,  $\frac{1}{4}$  mile distant from Juda prairie. The second column lists per cent presence in 5 prairies which are within a radius of three miles of Juda prairie. All of these 5 prairies are within the same mesic-*o* continuum interval (Curtis, 1955) as Juda prairie, and can, therefore, be expected to be fairly similar to it in compositional make-up. Column three shows per cent presence within 5 maple-basswood forests which are also within a radius of three miles.

As is evident from table 2, Juda prairie is fairly similar to neighboring prairies in its species composition. There are 11 instances of Juda plants, however, which are found in none of the neighboring prairies but are found in 4 or 5 of the neighboring maple-basswood forests. In addition, there are 15 plants which are found in both the neighboring forests and prairies. Many of these species, as *Anemone quinquefolia*, *Arenaria laterifolia*, *Celastrus scandens*, *Fragaria virginiana*, *Geranium maculatum*, and *Heuchera richardsonii* have very wide ecologic amplitudes and can be found in many prairies as well as in pioneer to climax forest. Others, as *Sanicula marilandica* (and in other areas, *Cardamine bulbosa* and *Viola cucullata*) are more limited, and grow in intermediate to climax forest and in meadows and moist prairie. There are several forest plants, however, as *Cornus racemosa*, *Polemonium reptans*, and *Polygonatum canaliculatum* which might indicate that the neighboring prairies were also at one time climax forest, but that they have lost a greater complement of their original understory forest cover than has Juda prairie. *Polemonium reptans* is included in this list since, although it is not present in the 5 Juda area forests, it is present in many maple-basswood forests in Wisconsin.



TABLE 2.—Presence list—Juda Prairie

	NF	%PP	%PF*		NF	%PP	%PF
<i>Allium canadense</i>		00	00	<i>Heracleum lanatum</i>		00	00
<i>Allium tricoccum</i>	*	00	100	<i>Heuchera richardsonii</i>		40	20
<i>Ambrosia trifida</i>		00	00	<i>Hydrophyllum virginianum</i>	*	00	100
<i>Andropogon gerardi</i>		100	00	<i>Lactuca canadensis</i>		60	00
<i>Anemone canadensis</i>		20	00	<i>Monarda fistulosa</i>		100	00
<i>Anemone cylindrica</i>		60	00	<i>Osmorhiza claytoni</i>		00	100
<i>Anemone quinquefolia</i>		20	80	<i>Oxalis violacea</i>		20	00
<i>Apocynum androsaemifolium</i>		20	00	<i>Oxypolis rigidior</i>		20	00
<i>Apocynum cannabinum</i>		20	00	<i>Parthenocissus vitacea</i>	*	20	100
<i>Arenaria lateriflora</i>		20	20	<i>Poa pratensis</i>		—	00
<i>Arisaema triphyllum</i>	*	00	100	<i>Podophyllum peltatum</i>	*	00	100
<i>Asclepias syriaca</i>		80	00	<i>Polemonium reptans</i>	*	40	00
<i>Aster azureus</i>		80	20	<i>Polygala senega</i>		60	00
<i>Aster ericoides</i>		80	00	<i>Polygonatum canaliculatum</i>	*	20	80
<i>Aster laevis</i>		60	00	<i>Prenanthes alba</i>		00	80
<i>Aster novae-angliae</i>		40	00	<i>Prunus virginiana</i>	*	00	80
<i>Aster sagittifolius</i>		20	20	<i>Pycnanthemum virginianum</i>		60	00
<i>Astragalus canadensis</i>		00	00	<i>Ratibida pinnata</i>		80	00
<i>Baptisia leucantha</i>		80	00	<i>Rhus glabra</i>		80	00
<i>Calamagrostis canadensis</i>		60	00	<i>Rhus radicans</i>		20	40
<i>Celastrus scandens</i>	*	20	40	<i>Rudbeckia subtomentosa</i>		20	00
<i>Cicuta maculata</i>		20	00	<i>Sanguinaria canadensis</i>		00	80
<i>Cirsium discolor</i>		80	00	<i>Sanicula marilandica</i>		20	20
<i>Comandra richardsoniana</i>		80	00	<i>Saxifraga pennsylvanica</i>		00	00
<i>Cornus racemosa</i>		40	40	<i>Silene stellata</i>		40	00
<i>Corylus americana</i>		100	20	<i>Silphium integrifolium</i>		80	00
<i>Desmodium illinoense</i>		60	00	<i>Silphium perfoliatum</i>		20	00
<i>Dioscorea villosa</i>		00	00	<i>Smilacina racemosa</i>	*	00	100
<i>Dodecatheon meadia</i>		60	00	<i>Smilax herbacea</i>	*	20	80
<i>Elymus canadensis</i>		80	00	<i>Solidago gigantea</i>		20	00
<i>Equisetum arvense</i>		20	00	<i>Solidago graminifolia</i>		20	00
<i>Equisetum laevigatum</i>		20	00	<i>Solidago rigida</i>		60	00
<i>Euphorbia corollata</i>		100	00	<i>Spartina pectinata</i>		40	00
<i>Fragaria virginiana</i>		100	20	<i>Spirea alba</i>		60	00
<i>Galium boreale</i>		60	00	<i>Stachys palustris</i>		40	00
<i>Galium concinnum</i>		00	100	<i>Steironema ciliatum</i>		20	00
<i>Gentiana andrewsii</i>		60	00	<i>Thalictrum dasycarpum</i>		60	00
<i>Gentiana flavida</i>		20	00	<i>Trillium recurvatum</i>	*	00	80
<i>Geranium maculatum</i>	*	40	100	<i>Urtica dioica</i>		00	00
<i>Helianthus grosseserratus</i>		80	00	<i>Veronicastrum virginicum</i>		40	00
<i>Helianthus laetiflorus</i>		80	00	<i>Vitis vulpina</i>		40	00
<i>Heliopsis helianthoides</i>		20	00	<i>Zizia aurea</i>		40	00

\* NF indicate presence in a nearby maple-basswood forest. %PP is per cent presence in 5 neighboring prairies of a comparable continuum position. %PF is per cent presence in 5 neighboring maple-basswood forests not including the immediate neighbor of the first column.

Juda prairie extends for nearly a mile between a road and a railroad track, and has been left relatively undisturbed as is evident from table 2 which shows only two foreign plants, *Poa pratensis* and *Urtica dioica* and two native adventurers or pioneers, *Ambrosia trifida* and *Silene stellata*. To the immediate north of Juda prairie, there are several miles of continuous true prairie without trees or tree grubs (in the sense of Muir, 1913) present. Some of this prairie

is still preserved. To the immediate south of Juda prairie is a pasture, and on the top of a moraine, about one-eighth mile distant is a maple-basswood forest. Bordering the forest to the north, between the forest and the western part of the prairie, are several large open-grown *Quercus macrocarpa*. Large old bur oaks are often found in similar situations in the Middle West; other examples are at Onarga, Illinois, and north of Urbana, Illinois. These oaks often form a narrow zone around the north and east sides of the forest, and perhaps performed the same protection from fire (which rarely came, because of prevailing westerly winds, from either the north or east) as did the much more extensive bur oak buffers to the south and west of the groves. The fact that large bur oaks appear between the maple-basswood forest and Juda prairie is evidence that the forest did not extend to the present location of the prairie, at least not in the immediate past. The presence of forest herbs today is probably not due to a forest occupancy within the time of European man (the last 100-150 years).

The probability of the species having entered the prairie by migration from the maple-basswood forest on the moraine seems to be more unlikely than the probability of the species surviving from a former climax forest occupancy since, if the odds for any one species entering and surviving in prairie are low, then the chance of 11 species being found in the same stand seems extremely remote.

The unlikelihood of plants of climax forest migrating into prairie can be shown from some characters in their life history. The species for which data on such characters are available in Randall (1952) are marked with an asterisk in table 1. Randall considers 6 of the 10 species to belong to taxonomic groups which are stable and conservative as to recent evolution, 2 are classified as intermediate, and 2 as unstable. Few of the species are likely to pioneer, since only 2 have fleshy fruits, none have stick tights, small and light seeds, plumed seeds or winged seeds, while 3 have elaiosomes and are disseminated by ants, one is explosive, and 4 have no special method. As observed by Gleason (1912), most of these species are normally vegetative reproducers and do not usually set seed. Of the 10 species, 8 have vegetative reproduction by rhizomes or detached parts. Essentially, then, the plants of table 1 and the 11 climax forest species of table 2 are relatively immobile, and are not likely to leave forest and migrate through a possible intervening savanna into a prairie where the chances of germination are not great and where a lack of foreign plants or domestic adventurers indicates stability with a resistance to invasion.

An examination of characters (from Randall, 1952) which might be advantageous to forest plants in prairie survival shows all of the 10 species marked in table 1 to be herbaceous perennials, 2 have bulbs as overwintering organs, 3 have corms, and 5 have rhizomes, while 8 are cryptophytes and 2 are hemicryptophytes. Four of the 10 species are vernal photosynthesizers, while the remainder are green throughout the season. The majority of these latter species probably complete most of their photosynthesis before mid-summer. The species do not suffer, therefore, from the late summer and fall shading of grasses, but as in climax forest, undertake photosynthesis in full sunlight.

The species die to ground level in late spring or early fall, and in so doing, as was noted by Gleason, escape fall fires. This escape is possible since the usually rapid movement of fire through dry grass results in soil temperatures being only slightly raised during burning. Late spring fires would kill the herbs above ground, but there is evidence that if this happens, the underground parts might still survive. In Wisconsin, there are forests highly dominated by *Quercus borealis* which have apparently originated from a fire degradation of maple-basswood forest (Curtis, 1954). In these forests, the understory plants are often climax species, and are not the species, or are not species in the same proportions, as are usually found in the intermediate continuum position in which red oak predominates. Fire of sufficient intensity to convert maple-basswood forest to red oak forest was, therefore, apparently not able to destroy the climax forest herbs.

If a climax forest were destroyed by fire and there was a subsequent prairie invasion, the soil conditions under prairie are little different from those which had previously existed in the forest. An analysis of a prairie soil and a climax forest soil in Wisconsin by Pierce (1951) show them to be remarkably similar in chemical and physical properties. A list of chemical features of soils in prairie with a few scattered trees and in climax forest also shows a close similarity (Bray, 1955). An occurrence of many species of soil microfungi in both prairie and climax forest is evident from an examination of the tables in Orpurt (1954) and Tresner, Backus, and Curtis (1954). A further factor in prairie survival by forest species is, therefore, the similarity in soil conditions, as noted. This factor, together with other microenvironmental similarities, as light intensity during the growing season, indicates that the environment of forest understory mesophytes is probably not too different in prairie and forest and that the problem of their prairie distribution is mainly an historic one.

The documentation of the available evidence of climax forest herbs in prairie gives support to Gleason's theory of a forest extent which was greater in the past, and to his conclusion that the prairie groves may be in many cases remnants and not recent invaders. The destruction by draining and farming of the poorly drained prairie flatlands of the central Middle West makes it difficult to gather further evidence, using the relict method, or whether the entire area, or large portions of it, was forested at some earlier post-Glacial and presumably pre-Xerothermic period.

#### SUMMARY

The presence of climax forest herbs in prairie in the Middle West was investigated by field surveys and from correspondence with taxonomists and ecologists in the region. Twenty-one species were noted in one or more prairies which could be considered climax forest herbs from their high presence in maple-basswood forest and their absence or low presence in pioneer oak forest. A detailed study of Juda prairie in southern Wisconsin showed eleven species which occurred in neighboring maple-basswood forests but not in neighboring prairies. These species were considered to be either survivors from a former forest occupancy or invaders from a nearby forest. Examination of features in the life history of the species suggested they are relatively

non-aggressive, immobile plants. The ability of the species to survive burning and to complete photosynthesis before shading by grasses was considered a factor in their survival in prairie. A possible similarity in microenvironment in prairie and forest was noted in relation to soil and to light intensity during the early growing season. This similarity emphasized the importance of an historic explanation of the presence of forest herbs in prairie. It was considered that additional support has been given Gleason's theory of a forest extent which was greater in the prairie peninsula region in the recent post-Glacial past.

## REFERENCES

- BRAY, J. R. 1955—The savanna vegetation of Wisconsin and an application of the concepts order and complexity to the field of ecology. Ph.D. Thesis. Univ. of Wis.
- BRENDEL, F. 1887—Flora Peoriana. Peoria, J. W. Franks and Sons.
- CONARD, H. S. 1956—Personal communication.
- CURTIS, J. T. 1954—Personal communication.
- 1955—A prairie continuum in Wisconsin. *Ecology* 36:558-566.
- , H. C. GREENE, AND J. R. BRAY 1955—Data on file with the Ecology Laboratory, Univ. of Wis.
- AND R. P. MCINTOSH 1951—An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476-496.
- FELL, E. W. 1955—Personal communication.
- GILBERT, M. L. 1953—The phytosociology of the understory vegetation of the upland forests of Wisconsin. Ph.D. Thesis. Univ. of Wis.
- GLEASON, H. A. 1912—An isolated prairie grove and its phytogeographical significance. *Bot. Gaz.* 53:38-49.
- 1952—The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Lancaster Press, Inc., Lancaster, Penna. 3 vols.
- HILGARD, E. W. 1915—Botanical features of the prairies of Illinois in ante-railroad days. Manuscript deposited with the library of the Illinois Historical Survey. Univ. of Ill.
- JACKSON, R. C. 1956—Personal communication.
- KIBBE, A. L. 1952—A botanical study and survey of a typical mid-western county: Hancock County, Illinois: covering a period of 119 years, from 1833-1952. Carthage, Ill.
- MUIR, J. 1913—The story of my boyhood and youth. New York.
- ORPURT, P. A. 1954—Studies on the soil microfungi of Wisconsin prairies. Ph.D. Thesis. Univ. of Wis.
- PIERCE, R. S. 1951—Prairie-like mull humus, its physico-chemical and microbiological properties (a contribution to the classification of forest humus). *Soil Sci. Soc. Amer. Proc.* 15:362-364.
- RANDALL, W. E., JR. 1952—Interrelations of autecological characteristics of forest herbs. Ph.D. Thesis. Univ. of Wis.
- STEARNS, F. W. 1956—Personal communication.
- STEYERMARK, J. A. 1955—Personal communication.
- TRANSEAU, E. N. 1935—The prairie peninsula. *Ecology* 16:423-437.
- TRESNER, H. D., M. P. BACKUS, AND J. T. CURTIS 1954—Soil microfungi in relation to the hardwood forest continuum in southern Wisconsin. *Mycologia* 46:314-333.

# Plants of a Northern Illinois Sand Deposit<sup>1</sup>

Egbert W. Fell

303 Penfield Place, Rockford, Illinois

In Rockton and Shirland townships in the northern part of Winnebago County, Illinois is a sand area of considerable size. It is within the oak-hickory association at the southern border of the white pine belt and at the northern border of the Prairie Peninsula. The sand plains and dunes contain a number of well developed, shallow Sphagnum bogs giving habitats that are unusual in Illinois. The vegetation of the area was given some consideration by Gleason (1910) nearly 50 years ago and it has remained much the same until recently farming and road building have made profound changes and it is thought that a record of the peculiar plant life should be made before it disappears entirely.

The area is twelve miles long and four miles wide (fig. 1). It extends from Rock River on the east to Sugar River on the west and since the sand does not extend far into Wisconsin the state line is arbitrarily taken as the northern border. On the west and south sides is the two mile wide, flat floor of Glacial Lake Peconica through which run Sugar and Peconica rivers to unite at Shirland before joining Rock River at Rockton (Salisbury and Barrow, 1918). The shore line of the glacial lake is at the 740 foot level and is easily followed. It is but little above the wide flat bottom of Coon Creek which bisects the area north and south. It is within this low bottom that most of the shallow bogs occur. The average elevation of the area is 775 feet, the hilly, wooded west half being 125 feet higher. The east half is a sand plain that is 50 feet above Rock River the bluffs of which have a large gravel element. The bluffs of Sugar River, on the west, average 50 feet and are pure, fine, yellow sand. Galena and Platteville dolomite, the bed rock, is very near the surface, being covered by a thin layer of gravelly clay or directly by sand. The only other rock is St. Peter sandstone which outcrops on Sugar River from the forest preserve north for one mile.

## GEOGRAPHICAL AFFINITIES OF THE PLANTS

There are many northern plants in the area the following being characteristic species:

<i>Lycopodium lucidulum</i>	<i>C. lacustris</i>
<i>Dryopteris cristata</i>	<i>C. lasiocarpa</i>
<i>Hierochloa odorata</i>	<i>C. sartwellii</i>
<i>Eleocharis palustris</i>	<i>C. siccata</i>
<i>Eriophorum angustifolium</i>	<i>C. substricta</i>
<i>Carex bebbii</i>	<i>C. tenera</i>

<sup>1</sup> The plant names are, with few exceptions, those of Jones and Fuller (1955). There are deposited in the State Museum in Springfield specimens of all the species that grow in the area, except weeds and very common natives. Only the more important plants are named in the lists. Dr. George D. Fuller, Curator of the Herbarium, Illinois State Museum, was of much help with the determinations.





<i>Juncus brachycephalus</i>	<i>L. ochroleucus</i>
<i>J. dudleyi</i>	<i>Epilobium adenocaulon</i>
<i>J. vaseyi</i>	<i>Cicuta bulbifera</i>
<i>Luzula multiflora</i>	<i>Angelica atropurpurea</i>
<i>Habenaria psycodes</i>	<i>Arctostaphylos uva-ursi</i>
<i>Maianthemum canadense</i>	<i>Pyrola elliptica</i>
<i>Salix candida</i>	<i>Vaccinium angustifolium</i>
<i>S. glaucophylloides</i>	<i>V. canadense</i>
<i>S. petiolaris</i>	<i>Viola pallens</i>
<i>Populus tremuloides</i>	<i>V. nephrophylla</i>
<i>Betula glandulifera</i>	<i>V. rugulosa</i>
<i>B. lutea</i>	<i>Lysimachia terrestris</i>
<i>B. pumila</i>	<i>Gentiana crinita</i>
<i>Parnassia glauca</i>	<i>G. procera</i>
<i>Ribes hirtellum</i>	<i>Galium trifidum</i>
<i>Geum triflorum</i>	<i>Campanula intercedens</i>
<i>Prunus pumila</i>	<i>C. uliginosa</i>
<i>Rubus pubescens</i>	<i>Lobelia kalmii</i>
<i>Amelanchier spicata</i>	<i>Solidago uliginosa</i>
<i>Lathyrus palustris</i>	<i>Aster junciformis</i>

Western plants are less common than those of the north but the following which do not grow much farther east are here:

<i>Paspalum stramineum</i>	<i>V. stricta</i>
<i>Cyperus schweinitzii</i>	<i>Hedeoma hispida</i>
<i>Juncus interior</i>	<i>Physalis virginiana</i>
<i>Mirabilis nyctaginea</i>	<i>Plantago purshii</i>
<i>Ribes ornatum</i>	<i>Ambrosia coronopifolia</i>
<i>Rosa suffulta</i>	<i>Vernonia fasciculata</i>
<i>Crataegus mollis</i>	<i>Kuhnia eupatorioides</i>
<i>Amorpha canescens</i>	<i>Liatris aspera</i>
<i>Petalostemum candidum</i>	<i>Boltonia recognita</i>
<i>P. purpureum</i>	<i>Rudbeckia subtomentosa</i>
<i>Viola pedatifida</i>	<i>Brauneria pallida</i>
<i>Oenothera rhombipetala</i>	<i>Helianthus maximiliani</i>
<i>Androsace occidentalis</i>	<i>Artemisia dracunculoides</i>
<i>Gentiana flavida</i>	<i>A. gnaphalodes</i>
<i>Acerates hirtella</i>	<i>A. ludoviciana</i>
<i>Lithospermum angustifolium</i>	<i>Lactuca ludoviciana</i>
<i>Verbena bracteata</i>	<i>Hieracium longipilum</i>

The following which extend into the northwest are also near their eastern limit here:

<i>Panicum perlongum</i>	<i>Acerates lanuginosa</i>
<i>Carex laeviconica</i>	<i>Physostegia speciosa</i>
<i>Quercus ellipsoidalis</i>	<i>Helianthus rigidus</i>
<i>Ranunculus rhomboideus</i>	<i>Liatris pycnostachya</i>
<i>Anemone ludoviciana</i>	<i>Aster ptarmicoides</i>
<i>Heuchera richardsonii</i>	<i>Senecio plattensis</i>
<i>Gentiana puberula</i>	<i>Agoseris cuspidata</i>

The following are peculiar in being confined to the Prairie Peninsula:

<i>Talinum rugospermum</i>	<i>Liatris cylindracea</i>
<i>Amelanchier interior</i>	<i>Solidago riddellii</i>
<i>Lespedeza leptostachya</i>	<i>S. media</i>
<i>Synthyris bullii</i>	<i>Artemisia serrata</i>
<i>Valeriana ciliata</i>	<i>Cirsium hillii</i>

The Atlantic coastal plain element (Peattie 1922) which is represented in the Indiana dunes by about 60 species is much less evident here since we have only the following:

<i>Panicum oligosanthos</i>	<i>J. scirpoides</i>
<i>Triplasis purpurea</i>	<i>Alnus rugosa</i>
<i>Hemicarpha micrantha</i>	<i>Polygonella articulata</i>
<i>Carex albolutescens</i>	<i>Lupinus perennis</i>
<i>Xyris tortia</i>	<i>Polygala cruciata</i>
<i>Juncus biflorus</i>	<i>Linaria canadensis</i>
<i>J. greenii</i>	<i>Gerardia purpurea</i>

The plants with southern affiliations are mostly wide spread species like *Woodsia obtusa*, *Asplenium platyneuron*, *Eragrostis hypnoides*, panicums, and *Lespedeza violacea*. There are some weedy immigrants like *Mollugo*, *Datura*, tumble-weeds, and smart-weeds beside older residents such as:

<i>Amorpha fruticosa</i>	<i>Proserpinaca palustris</i>
<i>Ptelea trifoliata</i>	<i>Isanthus brachiatus</i>
<i>Ludwigia palustris</i>	<i>Ruellia humilis</i>
<i>Oenothera laciniata</i>	

The greater part of the eastern mesophytes found in the county as a whole occur within this area but there are a few that are unaccountably absent though the proper habitat is here: *Erythronium albidum*, *Hepatica acutiloba*, *Mertensia virginica* (found in one place, obviously planted), *Amelanchier laevis*, *Cornus alternifolia*, and *Viburnum rafinesquianum*.

We lack many of the species found in active bogs in McHenry and Lake counties 25 miles to the east and in our latitude:

<i>Woodwardia virginica</i>	<i>Andromeda</i>
<i>Cypripedium reginae</i>	<i>Chamaedaphne</i>
<i>Drosera rotundifolia</i>	<i>Oxycoccus macrocarpus</i>
<i>Sarracenia purpurea</i>	<i>Menyanthes trifoliata</i>
<i>Rhux vernix</i>	

The following which are found on Mississippi River sand flats in our latitude and on Illinois River bottom sand below Peoria are absent here:

<i>Calamovilfa longifolia</i>	<i>Croton glandulosus</i>
<i>Aristida tuberculosa</i>	<i>Crotonopsis linearis</i>
<i>Commelina erecta</i>	<i>Callirhoe triangulata</i>
<i>Froelichia campestris</i>	<i>Opuntia rafinesquii</i>
<i>Cristatella jamesii</i>	<i>Monarda punctata</i>
<i>Strophostyles helvola</i>	<i>Diodia teres</i>
<i>Chamaesyce geyeri</i>	<i>Chrysopsis camporum</i>

#### PLANT HABITATS

##### HIGH PRAIRIE

Most of the area except Coon Creek bottom was formerly prairie but high prairie such as occupies the central part of the county is confined to small patches and most of it is either too sandy or too gravelly to be typical (Hopkins et al., 1916). There is a gravel prairie along Rock River bluff and there are sandy high prairies in the west part of the area in Shirland Town-

ship. There is one in Sections 1 and 36 and another between Sections 28 and 29 extending into Section 21. Beside these areas prairie plants are abundant in the edges of black oak woods and in openings within the woods. In these places such definitely high prairie species as *Carex umbellata* and *Anemone ludoviciana* occur as residuals. Prairie species are much less common in the mesophytic woods in Coon Creek bottom and they do not grow in the river bottom woods, but a number of high prairie plants are found in drying bogs.

The prairie grasses are a mixture of tall and mid-height species with an understory of low panicums, *Festuca octoflora*, *Aristida oligantha*, *A. basiramea*, *Sporobolus vaginiflorus*, and *S. neglectus*.

## SAND

*Plants of moving sand.*—The most important habitat is sand and many species are found here that are uncommon in northern Illinois. There is more or less activity in the sand all over the area but the main blowouts at the present time are in the southeast  $\frac{1}{4}$  of Section 28 and the west part of the southeast  $\frac{1}{4}$  of Section 4 Shirland Township. In these areas the usual succession is for quick growing annuals such as *Festuca octoflora*, *Triplasis purpurea*, *Setaria* spp., *Cenchrus pauciflorus*, *Digitaria sanguinalis*, *Bulbostylis capillaris*, *Ambrosia elatior*, *Amaranthus* spp., *Chenopodium* spp., and *Mollugo* with biennials such as *Oenothera biennis*, *O. rhombipetala*, *Linaria canadensis* and *Melilotus* spp., to be followed by perennial herbs and woody plants. This process is not infrequently shortened by the original invasion of vines, shrubs and trees. *Vitis*, *Rhus*, *Rosa*, *Robina*, and, in one instance, *Caragena* are examples, but the most common is black oak which not only colonizes bare sand but which, whatever the succession, occupies the apex of the evolutionary curve on the dunes at the present time.

The perennials involved in sand stabilizing are such herbs as:

*Equisetum hyemale*  
*Andropogon scoparius*  
*Sporobolus asper*  
*S. cryptandrus*  
*S. clandestinus*  
*Bouteloua curtipendula*  
*Panicum virgatum*  
*Leptoloma cognatum*

*Cyperus schweinitzii*  
*Carex pennsylvanica*  
*C. muhlenbergii*  
*Tephrosia virginiana*  
*Euphorbia corollata*  
*Lechea* spp.  
*Asclepias verticillata*  
*Acerates viridiflora*

The ligneous species are those already mentioned and *Salix humilis*, *Populus tremuloides*, *Corylus americana*, *Rubus* spp., *Prunus virginiana*, and *Ceanothus americanus*. Mat formers are important on a few of the dunes the most important being *Carex pennsylvanica* and *Polytrichum commune* which cover large areas to the exclusion of other growth. Less important are *Antennaria* spp., *Selaginella rupestris*, unidentified mosses, and fungi and lichens such as *Geaster* and *Cladonia*.

*Plants of quiet sand.*—These are the ones that are usually thought of as "psammophytes." Many, like those mentioned above, also grow on more disturbed sand and to some extent in the upland sand woods but the

preferred habitat is flat areas of quiet sand like the sand plain west of Rockton (Sand Prairie), near Sugar River west of Shirland, and the "20" sections of Shirland township north of Shirland. Besides the ones mentioned there are, among others, these:

*Koeleria cristata*  
*Panicum perlongum*  
*P. pseudopubescens*  
*P. scribnerianum*  
*Cyperus filiculmis*  
*Carex sicata*  
*Polygonum tenue*  
*Polygonella articulata*  
*Cassia fasciculata*  
*Lupinus perennis*  
*Polygala polygama*

*Chamaesyce glyptosperma*  
*Helianthemum bicknellii*  
*Viola pedata*  
*V. fimbriatula*  
*Asclepias amplexicaulis*  
*Phlox bifida*  
*Myosotis verna*  
*Isanthus brachiatus*  
*Hedeoma hispida*  
*Aster linariifolius*  
*Artemisia caudata*

#### SAND DUNE FOREST

The "true copies" of the original land survey made in the 1830s, which are on file in the county court house in Rockford, show that the hills between Coon Creek bottom and the dunes along Sugar River were occupied by a mixed oak-hickory growth similar to others over the county. The sand plain west of Rockton was not wooded and the black oak forest which now covers the dunes along Sugar River is of recent growth. These black oak groves do not have much litter, there is very little humus and they do not have a shrub border. These indications of the youth of this forest are confirmed by ring counting. The stumps in the new road-cut at Yale bridge indicate an age of about 85 years, most of them being less. This sudden growth of black oaks, which entirely changed the aspect of the dunes, is best accounted for by the decrease in fires that followed man's activity in road building and in farming. The location of the area, between rivers, is against fires having been large or frequent but the small ones that we have seen in recent years have had a very retarding effect on the vegetation. It is likely that a forest could not get started until this adverse influence was removed (Shimek, 1948, p. 165). The advance of the oaks over the bare sand, which still continues, is due to direct colonization brought about by the activities of squirrels, crows and bluejays. Seedlings are at too great a distance from bearing trees to be accounted for by gravity.

In this forest there are few trees except the black oaks. There is an occasional hickory, black cherry, or black locust but neither bur, Hill's nor red oak all of which are in other woods of the area. There are few shrubs: *Salix humilis*, *Corylus americana*, *Rubus* spp., *Prunus virginiana*, *Zanthoxylum americanum*, *Amorpha canescens*, *Arctostaphylos uva-ursi* (rare) and an occasional vine; *Smilax hispida*, *Rhus radicans*, *Vitis vulpina*, and *V. aestivalis*. Openings in the woods are numerous and the many prairie herbs in them are residuals that have not been entirely replaced by eastern forest plants.

The flora of the black oak woods is a mixture of eastern, western, and northern species and it can be reasonably assumed that this forest will be



succeeded by more mesophytic growth in the usual manner (Fuller, 1925). The following species are representative of the mixture:

<i>Selaginella rupestris</i>	<i>Petalostemum</i> spp.
<i>Botrychium obliquum</i>	<i>Gentiana flavida</i>
<i>B. multifidum</i>	<i>Lithospermum angustifolium</i>
<i>Cystopteris fragilis</i>	<i>Auricularia grandiflora</i>
<i>Woodsia obtusa</i>	<i>A. pedicularia</i>
<i>Asplenium platyneuron</i>	<i>Liatris cylindracea</i>
<i>Dryopteris spinulosa</i>	<i>Aster linariifolius</i>
<i>Andropogon</i> spp.	<i>A. ptarmicoides</i>
<i>Koeleria cristata</i>	<i>Krigia biflora</i>
<i>Paronychia canadensis</i>	<i>Silphium</i> spp.
<i>Talinum rugospermum</i>	<i>Hieracium longipilum</i>
<i>Anemone quinquefolia</i>	<i>H. scabrum</i>
<i>Cassia fasciculata</i>	<i>H. gronovii</i>

### WET AREAS

#### LOW PRAIRIE

Between Coon Creek and the wooded hills to the west are peaty, sandy areas which have a low prairie vegetation. Ditching and pasturing tend to change these to a drier type of prairie and recently plowing and cropping have begun. These areas are prolific flower producers, the plants being a mixture of prairie and eastern species. Native grasses, forbs and shrubs will quickly re-establish themselves (Shimek, 1948, p. 67) after a few years of cropping of low prairie areas which again become too wet to cultivate. This is due to re-seeding from adjacent areas, the growth of dormant seed and of perennial roots which have not been entirely destroyed. On a five acre tract which had been in crop for two seasons we saw, the third year that it lay fallow, the following species:

<i>Andropogon gerardi</i>	<i>Epilobium coloratum</i>
<i>Sorghastrum nutans</i>	<i>Thaspium trifoliatum</i>
<i>Cyperus strigosus</i>	<i>Cicuta maculata</i>
<i>Tradescantia ohioensis</i>	<i>Lysimachia quadriflora</i>
<i>Juncus macer</i>	<i>Scutellaria parvula</i>
<i>J. marginatus</i>	<i>Prunella vulgaris</i>
<i>J. torreyi</i>	<i>Pycnanthemum pilosum</i>
<i>Salix</i> (shrub spp.)	<i>Gerardia tenuifolia</i>
<i>Comandra umbellata</i>	<i>Galium pilosum</i>
<i>Thalictrum dasycarpum</i>	<i>Eupatorium perfoliatum</i>
<i>Anemone canadensis</i>	<i>Solidago gigantea</i>
<i>Veronicastrum virginicum</i>	<i>S. riddellii</i>
<i>Rorippa palustris</i>	<i>Rudbeckia hirta</i>
<i>Heuchera richardsonii</i>	<i>R. laciniata</i>
<i>Potentilla monspeliensis</i>	<i>Gnaphalium obtusifolium</i>
<i>P. simplex</i>	<i>Silphium laciniatum</i>
<i>Rosa carolina</i>	<i>S. integrifolium</i>
<i>Viola sagittata</i>	<i>Brauneria pallida</i>
<i>Lythrum alatum</i>	<i>Prenanthes racemosa</i>

Some areas that were plowed but not planted were first invaded by *Bidens coronata*, *B. cernua* and species of *Polygonum*. One was covered with *Eleocharis obtusa* and *Cyperus rivularis*; one that dried quite well by midsummer

showed an almost pure growth of *Bulbostylis capillaris*; one after being fallow for several years, had a dense growth of *Sarothra gentianoides*.

#### SHALLOW BOGS

There are a number of areas of deep peat, mostly in Coon Creek bottom, but there is none in process of active bog formation at the present time, which accounts for the absence of many of the Lake County species. Some of the bogs are well along toward being changed to low prairie by lowering of the water level, but there are still good examples of *Sphagnum-Eriophorum-Carex* bogs. There is no muck in these, as there is in prairie sloughs and sedge marshes, because muck is not formed from sand and peat. The following, more characteristic of dry soil, are abundant in the bogs:

*Agrostis hyemalis*  
*Panicum* spp.  
*Geum triflorum*  
*Polygala verticillata*

*Lechea stricta*  
*Phlox pilosa*  
*Gnaphalium obtusifolium*  
*Antennaria neglecta*

There are many other prairie species, and such deciduous forest species as *Arenaria lateriflora*, *Anemone quinquefolia*, *Polygala senega*, *Pedicularis canadensis*, *Aster cordifolius*, and *Hieracium canadense* are common.

The bogs were never wooded nor did they ever support an upland prairie flora so the forest and dry soil plants must be looked upon as invaders rather than as remnants of a former vegetation. With a farther lowering of the water table the whole area will become low prairie followed in turn by dry prairie, which succession is hinted at by the presence of prairie species; or there may be an invasion of bur oak giving rise in the not distant future to mesophytic oak woods. Prairie and/or forest plants will take the place of the northern and other old residents which have a narrower temperature and moisture tolerance.

The vegetation in all the bogs has been greatly disturbed in the past few years. The following are some of the better preserved areas, only the more unusual species of each being mentioned:

(B1) Two and one-half miles west of South Beloit in the NE.  $\frac{1}{4}$  of the NE.  $\frac{1}{4}$  of Section 3 Rockton Township is a shallow bog of 10 acres that was not grazed until 1948. It is typical of the bogs of the area, having a *Sphagnum* base and being well covered with *Carex*, *Eriophorum*, and *Juncus*. The following ferns are found here:

*Osmunda regalis*  
*O. cinnamomea*  
*O. claytoniana*  
*Oncoclea sensibilis*

*Dryopteris thelypteris*  
*D. cristata*  
*Athyrium angustum*

There are also these unusual species:

*Eriophorum angustifolium*  
*Scleria triglomerata*  
*Carex substricta*  
*C. emoryi*  
*C. brachyglossa*

*Juncus vaseyi*  
*J. marginatus*  
*J. scirpoides*  
*J. acuminatus*  
*Aletris farinosa*

*Habenaria lacera*  
*Calopogon pulchellus*  
*Salix glaucophylloides*  
*S. candida*  
*S. petiolaris*  
*Rubus pubescens*  
*Aronia melanocarpa*

*Polygala cruciata*  
*Oenothera laciniosa*  
*Bartonia virginica*  
*Castilleja coccinea*  
*Galium trifidum*  
*Aster junciformis*  
*Helianthus giganteus*

(B2) In the SW.  $\frac{1}{4}$  of Section 3 Rockton Township is a decadent bog of five acres where *Sphagnum* is largely replaced by *Polytrichum* though there is still some water. The rushes and sedges are giving away to shrubs: the bog willows, *Betula pumila*, *B. lutea* (rare), *B. glandulifera*, *Aronia prunifolia*, *Spiraea alba*, *Rhamnus frangula*, *Gaylussacia baccata*, *Vaccinium angustifolium*, and *V. corymbosum*. This bog is in a valley between low sand ridges that are covered with mixed oaks, mostly large black oaks, that grow to the edge of the bog. The few small oaks that are in the bog are bur oak, the black oaks have not invaded.

(B3) A bog on the Campbell farm occupies the greater part of the SE.  $\frac{1}{4}$  of Section 9 and the SW.  $\frac{1}{4}$  of the SW.  $\frac{1}{4}$  of Section 10 Rockton Township. It is still quite wet being fed by springs which afford good evidence of the low temperature of the bog. The more protected parts have abundant *Sphagnum* with *Eriophorum*, *Carex* and such grasses as *Panicum implicatum*, *Hierochloa odorata*, *Muhlenbergia glomerata*, *M. racemosa*, and *Spartina pectinata*. In places that are getting dry *Polytrichum commune*, *Cyperus rivularis*, and *Eleocharis obtusa* flourish and will no doubt be succeeded by *Bulbostylis capillaris* and *Sarothra gentianoides* whose water requirements are less. Part of this bog is well supplied with shrub willows and dwarf birch and there are a few other shrubs as *Spiraea*, *Aronia* and *Viburnum* but there are no trees except an occasional small poplar, elm or bur oak. Some of the unusual species found here are:

*Carex albolutescens*  
*Juncus canadensis*  
*J. brachycephalus*  
*Xyris torta*  
*Spiranthes cernua*

*Parnassia glauca*  
*Gentiana crinita*  
*G. procera*  
*Valeriana ciliata*  
*Solidago uliginosa*

The proximity of a bur oak woods with sandy, peaty soil, a dense shrub border and residual bog species suggests that this will be the succession here.

(B4) In the SE.  $\frac{1}{4}$  of Section 20 Shirland Township is a boggy area of 10 acres bordered on one side by sandy upland prairie and on the other by a Sugar River slough with tall grasses and sedges. It has but little *Sphagnum* but *Polytrichum* and *Rubus hispidus* form a thick mat over nearly the whole area. Notable species are: *Maianthemum canadense*, *Botrychium obliquum* and *B. dissectum* both growing in small colonies, *Osmunda regalis*, *O. claytoniana*, and *Dryopteris spinulosa*. The shrubs are *Aronia melanocarpa*, *Alnus rugosa*, *Betula pumila*, *Ilex verticillata*, and *Vaccinium canadense*. A tall blackberry is invading.

(B5) In the SW.  $\frac{1}{4}$  of Section 23 Shirland Township is an intradunal bog in process of extinction. In recent years the several potholes have been dry

by mid-summer. *Gaylussacia* is the dominant shrub with a mat of *Polytrichum* and *Rubus hispidus*. *Vaccinium* is absent but there is still the remains of a bog flora: *Osmunda regalis*, *Juncus greenii*, *Scirpus* spp., *Xyris torta*, *Polygala cruciata*, and bog willows. Prairie and sand plants are invading:

*Salix humilis*  
*Polygonum tenue*  
*Rosa carolina*  
*Potentilla arguta*  
*Polygala polygama*

*Lechea* spp.  
*Helianthemum* spp.  
*Acerates hirtella*  
*Viola pedata*  
*V. pedatifida*

These will doubtless be followed by prairie grasses, *Amorpha canescens*, *Lespedeza hirta*, *L. capitata*, *L. leptostachya*, *Ceanothus americanus*, *Lithospermum* spp., and *Silphium* spp. from the contiguous dry areas. This bog is between sand ridges covered with black oak. That this will follow the invading prairie is indicated by seedlings. There are no seedling bur oaks. In the foreseeable future a dune forest will result, black oak with persisting prairie species, this to be succeeded by mesophytic growth in the usual way.

#### WOODS OF THE BOG AREA

In the lower part of Coon Creek bottom, Campbell woods, the NW.  $\frac{1}{4}$  of the SE.  $\frac{1}{4}$  of Section 16 Rockton Township, and some adjacent patches are nearly virgin. This wood is definitely mesophytic but is not of the wet bottom land type, having no button-bush or soft maple. The large trees are mostly white oak and bur oak mixed with elm, linden, hackberry, black cherry and hickory. Under-story trees, shrubs and vines are abundant and the shrub border is dense. The herbs are eastern and northern species:

*Botrychium obliquum*  
*Osmunda regalis*  
*O. claytoniana*  
*Dryopteris spinulosa*  
*D. thelypteris*

*Cypripedium parviflorum*  
*Pyrola elliptica*  
*Polygala sanguinea*  
*Gerardia purpurea*  
*G. tenuifolia*

There are few prairie species. That this bur oak woods followed the bog directly (Gleason, 1910) is hinted at by the presence of the bog species which appear to be residuals.

#### SUMMARY

The vegetation of the sand deposit in northern Winnebago County, Illinois was reviewed by Gleason in 1910. This article is a record of that vegetation which is rapidly disappearing. The area is described, its limits, phyto-geographical location and main physical features being given.

Important extraneous species are listed and peculiarities of distribution noted: Many northern plants are in shallow bogs and sand hills; Atlantic coastal plain species are fewer than in Lake Michigan sand; a number of western and northwestern plants are here near their eastern limit; prairie species are invading the bogs; the black oak forest of the sand dunes has a large residual prairie flora; the mesophytic woods in the bog area has bog species which appear to be residuals.

The plants that are characteristic of the sand and of the peat areas are listed. Habitats not peculiar to the area are not considered.

The trend is toward deciduous forest as in all of northern Illinois but the sand and peat complicate the succession. In the sand black oak is dominant at the present time. It may invade bare sand directly or it may follow the prairie perennials which were preceded by annuals and biennials. Farther progress will be in a mesic direction.

In the bogs succession follows drying, the direction being determined by what plants with suitable requirements are present at the particular time. The usual cycle is from bog to prairie, to bur oak; or bur oak may follow bog directly. Black oak may follow prairie which has replaced bog and be replaced in turn by bur oak. A mixed mesic forest growth may directly follow bog and northern species.

The sudden destruction of a low prairie vegetation may be followed by a quick re-establishment if the disturbance is discontinued.

#### REFERENCES

- FULLER, G. D. 1925—The vegetation of the Chicago region. Univ. of Chicago.  
GLEASON, H. A. 1910—The vegetation of the inland sand deposits of Illinois. Ill. State Lab. Nat. Hist., Bull. 9:23-174.  
HOPKINS, C. G. ET AL. 1916—Winnebago County soils. Ill. Agri. Exp. Sta. Soil Report 12.  
JONES, G. N. AND G. D. FULLER 1955—Vascular plants of Illinois. Univ. of Ill. Press, Urbana and Ill. State Mus., Springfield, Ill. Mus. Sci. Ser., 6.  
PEATIE, D. C. 1922—The Atlantic coastal plain element in the flora of the Great Lakes. *Rhodora* 24:57-70, 80-88.  
SALISBURY, R. D. AND H. H. BARROWS 1918—The environment of Camp Grant. Ill. Dept. of Reg. & Ed. State Geog. Sur. Bull. 39.  
SHIMEK, B. 1948—The plant geography of Iowa. U. of Iowa Stud. in Nat. Hist. Ser. 417:1-178.



# Succession on River Alluvium in Northern Alaska<sup>1</sup>

L. C. Bliss

*University of Illinois, Urbana*

J. E. Cantlon

*Michigan State University, East Lansing*

During the summer of 1953, a study was made of the vegetation adjacent to several of the major rivers on the Arctic Slope of Alaska. Much of the descriptive work and all of the quantitative sampling included here were carried out along the Colville River near Umiat, Alaska (N 69° 22', W 152° 08'; elevation approximately 350 feet). These data were supplemented through observations by the second author at several other points on the Arctic Slope. This portion of Alaska, except possibly under the deeper lakes, is underlain by continuous permafrost. The vegetation of the region, except on and immediately adjacent to the river floodplains, is composed of one or more, usually several, of the various tundra plant communities (Spetzman 1951, Cantlon & Bormann 1953, Churchill 1955, Bliss 1956). On the floodplains and lower terraces, plant communities occur in which the plants are both of a lower life-form and of a somewhat higher life-form than the adjoining tundra communities. These are, respectively, the open, perennial-herb pioneer community and the tall (up to 20 feet), fairly dense, feltleaf willow (*Salix alaxensis*<sup>2</sup>) communities. Both are of successional status and as the direct influence of the river becomes less through meander migration, they give way by stages to one of the several tundra types that are not dependent upon the river influence. The object of the present study is to describe in a preliminary way the zonation and apparent successional relationships of the vegetation along rivers in the area.

Appreciative acknowledgment is made to Dr. Howard A. Crum and Dr. Lewis E. Anderson for identification of the bryophytes and to Dr. William L. Culberson for identification of the lichens.

## REVIEW OF THE LITERATURE

Arctic and sub-arctic alluvial communities in North America have been described by a number of authors among whom may be mentioned Griggs (1936), Hanson (1951, 1953), Hopkins and Sigafos (1950) and Raup (1935). Alluvial succession is described for several places in this region including the Arctic Slope of Alaska (Spetzman 1951), rivers along the Canol Road in southeastern Yukon (Porsild 1951), lower and central Yukon River, Alaska (Baxter and Wadsworth 1939, Benninghoff 1952) and on the Kuskokwim River, Alaska (Drury 1956).

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<sup>2</sup> Nomenclature, except where authorities are given, follows that of Hult  n (1941-50), for vascular plants, Grout (1940) for mosses and Hale and Culberson (1956) for lichens.

In the Sub-Arctic, the non-aquatic alluvial successions are described as forming a sequence from various pioneer vegetation through feltleaf willow to poplar-willow-birch to spruce. Benninghoff (1952) and Drury (1956) describe a decrease in depth of thaw with increasing distance from the stream channel and point out that this decrease is associated with the improved insulation of the surface by the vegetation of the late stages of the sere. Drury also says that the tall stream-side forest of white spruce gives way on the terraces to mosaics of black spruce muskeg, shrub and cotton grass tussock tundra, sedge marsh, and ponds as drainage deteriorates following the development of the permafrost layer.

In the tundra region on the Arctic Slope of Alaska, Spetzman (1951) has briefly outlined the major stages in alluvial succession as it occurs on the major rivers. He notes that tundra vegetation of various sorts replaces the alluvial shrub types as the depth of thaw decreases.

For arctic and sub-arctic areas outside of North America, alluvial zonation and succession are perhaps better known. Some of the papers particularly pertinent to the present study include that of Polunin (1936) for Norwegian Lapland and the following Siberian works: Sheludiakova (1938) for the Indigirka River, Sochava (1933) for the Anabar River, Vasilev (1936) for the Anadyr District, Aleksandrova (1937) for the Poigai River and Gorodkov (1944) for the Ob and Yenisei Rivers. Although these studies indicate certain floristic differences between the Siberian and the northern Alaskan regions, the similarities in flora, vegetation and successional sequences between the two regions are strong. In general, the successions on alluvial bars and banks seem to be initiated by a pioneer vegetation of perennial herbs, followed in areas of less flooding by shrubs which in turn are replaced by trees or by tundra meadow or marsh, depending upon the location. The species composition of the perennial herb pioneer vegetation and of the tundra meadows and marshes appear to be very much like their Alaskan counterparts. The tall shrub and tree species of the intermediate stages of the successions are related to but are mostly different species than the Alaskan ones.

Gorodkov (1944) in describing the tundras of the Ob-Yenisei divide of northwestern Siberia has discussed in considerable detail the nature of plant succession associated with alluvial sites. He considers the successions initiated on fresh alluvium to be of a secondary (mesotrophic) nature and points out that in their development, in connection with the evolution of the entire landscape, they tend to approach a single, but really diversified climax tundra of the western sector of the Arctic: the moss tundra. He describes the initial stages on sandy alluvium as simple, with rarely more than 10 species, and dominated by grasses and horsetail. The first shrubs to invade these flood-meadows are *Salix reptans* and *S. lanata*. This simple flood-meadow stage is replaced by a shrub-moss flood-meadow which has up to 15 species of moss, a few lichens, many grasses and sedges. The most important dwarf shrub is *Salix polaris*. The shrub layer, up to 50 cm tall, is mainly *Salix reptans* Rupr. and *S. lanata* Lightf. with some admixture of *Betula nana* and *Salix glauca*. This shrubby stage persists for a long time, eventually giving way to a shrub-moss subclimax type of the terraces. Southward nearer the northern wooded tundra the shrubs become taller and more varied.

Gorodkov emphasizes the role of silting and flood erosion in limiting the composition of the lower layers on the floodplain and points out the decrease in depth of thaw associated with the development of the sere. Many variations to this basic sequence are described and attributed to edaphic or other differences.

#### METHODS

All of the quadrat sampling and most of the descriptive studies were confined to a north-south transect line which ran from the edge of the Colville River on the south, across the floodplain, and up onto the first river terrace (fig. 1). The entire transect was approximately 1.5 miles long, of which over 2,000 feet were actually sampled.

The dominant layer of the major shrub communities and the ecotones between them were sampled using 125 1 x 5 m quadrats; within each the number and diameter of shrub stems was determined as was shrub height. A 1 m steel rod was used as a probe to determine depth to frozen soil or to coarse gravel at 1 m intervals along one side of each quadrat. A brief description of herbaceous cover, surface microrelief, and depth of thawed sand and silt on top of the gravel was recorded. The lower vegetation layers were sampled using only 8 small 0.5 x 2.0 m quadrats located in selected areas along the transect. On these, per cent cover was estimated for each species.

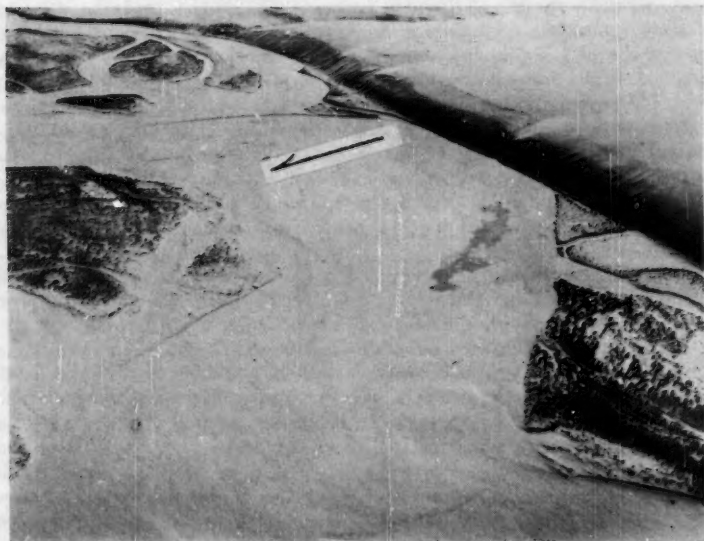


Fig. 1.—Aerial photo showing the study area on a large meander of the Colville River, Alaska. The feltleaf willow protrudes above the mid-April snow cover while the frozen river channel, bare gravel bars and pioneer herb areas are mantled with snow. The transect direction is marked by the arrow and continued on the first terrace which is out of picture at left. The upland on the right supports dwarf shrub-cottongrass tussock tundra meadow. Boston University photo.

Soil pits were dug at each of the smaller quadrats and stratification of the alluvial materials examined.

The quadrat sampling yielded density, frequency, and basal area data which are summarized in table 1. Basal area as used here refers to the basal

TABLE 1.—Summary of the density-frequency-dominance values for the three shrub communities. Both young and decadent feltleaf willow stands are confined to the main river gravel bar while the alder-willow-heath community is restricted to the terrace.

Young Feltleaf Willow Community (43 quadrats)				
	Density %	Frequency %	Dominance %	DFD
<i>Salix alaxensis</i> .....	71.1	86.0	94.6	251.7
<i>S. farrae walpolei</i> .....	13.6	18.6	1.5	33.7
<i>S. arbusculoides</i> .....	5.2	11.9	1.4	18.5
<i>S. glauca desertorum</i> .....	9.4	6.8	2.0	18.2
<i>S. richardsonii</i> .....	0.2	2.3	0.1	2.6
<i>S. murici?</i> .....				
<i>S. pulchra</i> .....				
<i>Alnus crispa</i> .....	0.5	4.7	0.4	5.6
Decadent Feltleaf Willow Community (50 quadrats)				
	Density %	Frequency %	Dominance %	DFD
<i>Salix alaxensis</i> .....	28.5	64.0	59.9	152.4
<i>S. farrae walpolei</i> .....	8.9	22.0	1.7	32.6
<i>S. arbusculoides</i> .....	28.0	46.0	11.1	85.1
<i>S. glauca desertorum</i> .....	17.2	26.0	7.6	50.8
<i>S. richardsonii</i> .....				
<i>S. murici?</i> .....	12.7	34.0	4.9	51.6
<i>S. pulchra</i> .....				
<i>Alnus crispa</i> .....	4.7	6.0	14.8	25.5
Alder-Willow-Heath Community (32 quadrats)				
	Density %	Frequency %	Dominance %	DFD
<i>Salix alaxensis</i> .....				
<i>S. farrae walpolei</i> .....				
<i>S. arbusculoides</i> .....	3.4	28.1	2.5	34.0
<i>S. glauca desertorum</i> .....	11.5	37.5	8.5	57.5
<i>S. richardsonii</i> .....	14.9	71.9	10.9	97.7
<i>S. murici?</i> .....				
<i>S. pulchra</i> .....	19.1	46.9	14.0	80.0
<i>Alnus crispa</i> .....	51.1	81.3	64.1	196.5

area of shrub stems approximately 30 cm above ground level. Density-frequency-dominance values (DFD) for each species result from adding density, frequency, and basal area percentages (Curtis 1947).

The background for comments on the general picture of alluvial succession for the Arctic Slope of Alaska was gained from ground reconnaissance in a number of sites in river valleys from the Arctic Coast south to the mountain front and from the Nigu and Meade Rivers on the west to the Colville and Chandler Rivers on the east. Further information was obtained from low-altitude aerial reconnaissance of river valleys from the Yukon Territory-Alaska boundary on the east to Cape Lisburne on the west and from the Arctic Coast south to the mountain front.

## RESULTS

### DETAILED STUDY ON THE COLVILLE RIVER AT UMIAT

The sampling substantiated the visual observation that the vegetation differed rather markedly over the transect from the river channel across the floodplain and up onto the first terrace level. Based upon these differences, four community types are recognized. These and their associated site characteristics are described below. Since the four types integrate and in places form continuous gradients from stream side to terrace, their separation is one of convenience.

### PERENNIAL HERB COMMUNITIES

Plant succession is initiated on bare floodplain gravels wherever small pockets of sand and silt accumulate among the rocks. Large areas of gravel lie adjacent to the river, forming banks and bars that are only slightly higher than the normal summer water level. The spring and summer floods add fresh alluvial material and erode existing pockets as a result of which new sites for plant establishment are constantly being added. The pioneer species appear to be able to maintain themselves in many of these sites as evidenced by the presence of previous year's flowering stalks and leaves even though these areas showed definite evidence of having been flooded. Ice abrasion during spring break-up is restricted to the lowest bars, and flood levels are reached after break-up ice has moved down stream.

The most abundant pioneer herb species include *Crepis nana*, *Erigeron purpuratus*, *Epilobium latifolium*, *Artemisia tilesii*, *A. alaskana*, *A. arctica*, *Oxytropis* sp., *Astragalus alpinus*, *A. lepagei* Hult. and *Lupinus arcticus*. Other herbs present but much less abundant are *Agropyron sericeum*, *Poa lanata*, *Deschampsia caespitosa*, *Hedysarum alpinum* ssp. *americanum*, *H. mackenzii* and *Cardamine richardsonii* (fig. 2).

While the structure of the above community is very open in response to the scattered distribution of habitable sites, local areas may support a more-or-less closed herbaceous cover. Such stands usually originate following the establishment of the first willow shrubs, most frequently *Salix alaxensis*. While a few seedling willows were observed, most of these pioneer shrubs are outgrowths from willow-containing clumps of river bank which cave into the stream and are subsequently stranded on the bars downstream. These clumps and the shrub growth from them accelerate the deposition of sand



and silt encouraging the development of more-or-less closed herbaceous communities dominated by *Lupinus arcticus*, *Oxytropis* sp., *Epilobium latifolium*, *Artemisia alaskana*, *A. tilesii* and *Astragalus lepagei*. To this group of open gravel pioneers is added *Aster sibiricus*, *Parnassia palustris* and *P. kotzebuei* (fig. 3). Other less common species usually restricted to areas of deeper sand and silt include *Papaver macounii*, *Stellaria monantha*, *Moehringia lateriflora*, *Arctagrostis latifolia*, *Bromus pumpellianus* var. *arcticus* and *Hierochloa odorata*.

Mosses become established in these perennial herb stands and may cover 20 to 40 per cent of the surface. With the exception of *Angstroemia longipes*, all mosses are sterile and belong to the genera *Bryum*, *Dicranum*, *Dicranella* and *Encalypta*. The lichen *Stereocaulon glareosum* var. *brachyphyllloides* is present in small amounts.

While *Salix alaxensis* is usually the first willow to become established, a few scattered shrubs of *Salix arbusculoides* and *S. glauca* ssp. *desertorum* may also occur.<sup>3</sup> In the study area, the greenleaf willows attain a height of 0.5 to 1.5 m on these outer bars while feltleaf willow ranges from 2 to 3.5 m in height.

Several areas were observed having a moderately heavy herb cover of similar species composition to the above but lacking the willow shrubs. In these sites the thicker mantle of sand and silt seemed to be due to the configuration of the floodplain as well as the action of the herbaceous plants themselves.

These herbaceous communities with and without willow are usually less than 1.5 m above the normal river level in mid-summer and as a result, it is not uncommon for parts of them to be torn out or nearly buried during periods of high water. The soil is thawed to a depth in excess of one meter early in July and there are indications (Maxwell 1954) that the top of the frozen zone may be as deep as 2½ m.

#### YOUNG FELTLEAF WILLOW COMMUNITIES

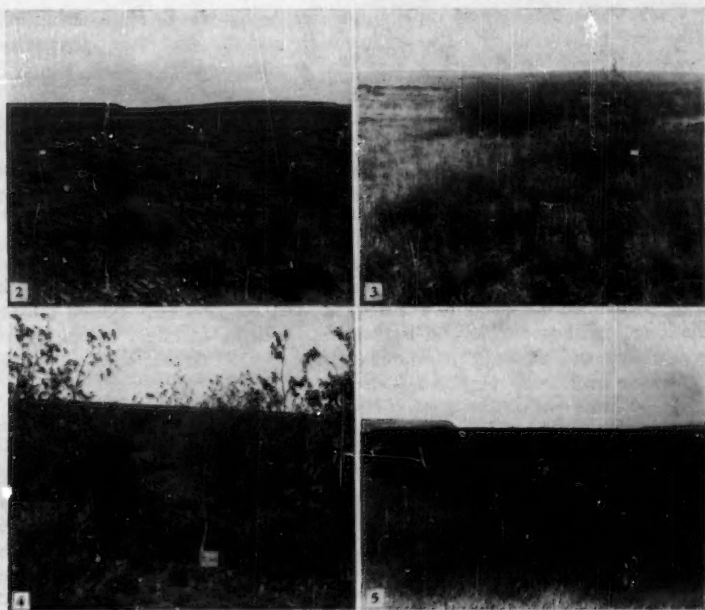
Young feltleaf willow communities occur at levels above those occupied by the perennial herb and pioneer willow stands described above. In the study area, a vigorous stand of tall feltleaf willow occupied the margins of an island-like bar that stood a few feet above the higher perennial herb stands (figs. 1 and 4). Stranded debris in the branches up to a height of 1 m indicates that this stand is inundated during high water. Along the outermost edges, where the impact of flooding is greatest, the willow clumps are scattered but vigorous, tall (3 to 4 m), and at 30 cm above the ground the stem diameters are from 5 to 10 cm. Dead stems are absent.

The soil, as exposed in a 2 m vertical cut-bank, showed the following profile: 0 to 0.7 m gravel and coarse sand, 0.7 to 1.4 m silty sand, 1.4 to 1.8 m medium gravel. The ground surface has much bare gravel and sand. By late July, the top of the frozen layer had retreated below the effective probing depth of 1 m.

<sup>3</sup> All willow species other than *Salix alaxensis* are collectively referred to as the greenleaf willow complex (Hanson 1953), although it is recognized that several of these species have gray-green leaves.

In the study area, the best development of feltleaf willow in terms of height and density occurs near the edges of the stand which are adjacent to the stream channel and usually on the up-stream end of the bar. It is these sites which receive the greater impact of the early flood waters. Better willow development is also noticeable along the small channels, which cut across the bars and are dry except in periods of high water.

The herb layer is dominated by scattered clumps of *Lupinus arcticus*, *Oxytropis* sp., *Hedysarum mackenzii*, *H. alpinum* ssp. *americanum*, *Artemisia tilesii* and *A. alaskana*. Other species present but much less abundant include *Aster sibiricus*, *Castilleja pallida*, *Taraxacum* sp., *Polemonium boreale*, *Astragalus americanus*, *A. lepagei*, *Deschampsia caespitosa*, *Agropyron sericeum*



Figs. 2-5.—2. Perennial herb community on floodplain of Colville River at Umiat, Alaska. The vegetation is primarily *Artemisia* spp., *Hedysarum* spp., *Lupinus arcticus* and various grasses. Note coarseness of gravels between and the accumulation of sand around the vegetation clumps. 3. Early stages of willow invasion of the perennial herb community. Note heavy grass and herb cover associated with the willow shrubs. The dark line in background is the edge of the first terrace which has a cover of alder at this location. 4. Vigorous young feltleaf willow on edge of transect nearest to perennial herb vegetation. Low greenleaf willow, lupine and grasses make up the understory. The swath through the stand in the middle of the photo is 2 m to left of transect line. 5. Vegetation on the edge of the first terrace above the floodplain of the Colville River. The dark shrubs are alder, the tall "grassy" area in foreground is sedge marsh and a small patch of tussocky tundra meadow occurs to the right of center. Boston University photos.

and *Poa lanata*. These later species are more frequently found where sand and silt have accumulated.

At greater distances from the stream channels and these scattered clumps of feltleaf willow, sand and silt have accumulated to greater depths. Here the stems of feltleaf are much closer together and frequently of greater height. The herbaceous cover, which ranges from 10 to 50 per cent, consists of *Lupinus arcticus* and a few scattered plants of *Agropyron sericeum* and *Deschampsia caespitosa* along with a moss cover that may range from 20 to 40 per cent. The main species of moss are *Drepanocladus uncinatus* and sterile *Bryum* sp., *Brachythecium* sp. and *Dicranella* sp. In addition to the heavy cover of feltleaf willow, there are a few greenleaf willows, *Salix farrae* ssp. *walpolei*, *S. arbusculoides*, *S. glauca* ssp. *desertorum* and *S. richardsonii*. *Alnus crispa* rarely occurs in these stands. The height of these willows and alder seldom exceeds 1 to 1.5 m. in the young feltleaf willow stands.

#### DECADENT FELTLEAF WILLOW COMMUNITIES

The decadent feltleaf willow community covers by far the largest area on the main bar. It is characterized by large scattered feltleaf willow clumps in which a high proportion of the stems are dead. Feltleaf willow still is clearly the dominant species (table 1.) but several of the greenleaf willows, some of which appear in the previous young feltleaf willows, community, contribute a significant amount of cover. Among these, *Salix arbusculoides* is most important followed by *S. muriei*?, *S. glauca* ssp. *desertorum* and *S. farrae* ssp. *walpolei*. The contribution of *Alnus crispa* has also increased but it is still the least important shrub. Feltleaf willow shrubs average 2 to 4 m in height while the associated but less important greenleaf willows seldom attain a height greater than 2 m. The larger feltleaf willow stems are 10 cm in diameter, 30 cm above the ground, and have up to 46 "annual" rings.

This community exhibits alternations in composition from place to place which are associated with microtopographically induced differences in soil drainage. The more extensive, level to slightly concave areas have less greenleaf willow in the shrub layer and the herb cover, contributed mostly by *Equisetum arvense* and *Pyrola grandiflora*, ranges from 20 to 50 per cent. Cover in the bryophyte layer is high, usually 80 to 100 per cent. The most important moss is *Drepanocladus uncinatus* and of minor importance are *Campylium stellatum*, *Pogonatum alpinum*, *Leptobryum pyriforme* and *Byrum* sp. Lichens, although occasionally encountered, are not important. The soil surface often has a few centimeters of peaty organic material and in such sites frozen soil was encountered between 0.5 and 0.7 m below the surface in late July.

The less extensive, higher and drier microtopographic sites have more greenleaf willow while feltleaf willow is represented by only a few partially dead clumps. *Alnus crispa*, although occasionally present on the moist sites, is not encountered on these convexities. The herb cover on these higher areas ranges from 10 to 30 per cent and consists of *Lupinus arcticus* and *Agropyron sericeum*, *Deschampsia caespitosa*, *Poa lanata* and small amounts of *Arctagrostis latifolia* and *Hierochloe odorata*. The moss cover is less (70 to 80 per cent) but is still contributed primarily by *Drepanocladus*

*uncinatus*. In late July frost was encountered between 0.8 and 1.0 m below the surface in several locations.

Areas intermediate in drainage between the two described occur, and the associated vegetation is of an intermediate character.

#### TERRACE COMMUNITIES

The transitions between the pioneer perennial herb community and the young feltleaf willow community and between the latter and the decadent feltleaf willow community are gradual in nature. However, at the site of the detailed study, the break between the decadent feltleaf willow of the floodplain and the alder shrub-dwarf heath meadow of the terrace is sharp. This break is associated with a near-vertical rise which marks the contact of the floodplain and the first of three well-marked alluvial terraces. Unlike the floodplain, the lower terrace is not subject to frequent, complete flooding although local low areas may be flooded each year.

The vegetation of the lower terrace has a predominantly shrubby physiognomy but it is actually a mosaic made up of several shrub, dwarf heath meadow and marsh types (fig. 5). These differences in vegetation are, in part, associated with soil differences such as variations in thickness of sand, silt and peat over the alluvial gravels or with the degree of surface drainage. However, the relationships are complex and differences in vegetation occur on sites that appear to have similar soil conditions. This lower terrace traversed an area that might be described broadly as open, alder-greenleaf willow shrub. Within this broad category, however, there are several variations, which differ in amount of shrub cover and nature of lower vegetation layers. These differences seem to be correlated, in part at least, with surface drainage.

At the site where the transect makes contact with the terrace, the vegetation is a shrub stand of varying density. The dominant shrub is *Alnus crispa* but *Salix richardsonii*, *S. pulchra*, *S. glauca* ssp. *desertorum*, *S. arbusculoides* and very small amounts of *Betula nana* ssp. *exilis* also occur. The height and density of the shrubs is greatest adjacent to the near-vertical drop to the floodplain. Here, shrub heights of 3 m were recorded and alder cover was 100 per cent. Farther back, alder cover had less than one-fourth that value and shrub heights seldom exceeded 1 m, the majority being 0.5 m.

The thickness of thawed soil, the active layer, is greater near the terrace edge. Here, frozen soil was encountered on August 25th at a vertical depth of 1 m, while 2 m back from the edge it was within 27 cm of the surface. Except along the edge, the thickness of the thawed layer ranged from 25 to 40 cm along the transect on the above date.

The soil-cut exposed in the terrace edge showed the following profile: surface to depth of 1.3 m, lenses of peat between layers of sand and silty sand, 1.3 to 1.5 m, coarse to medium gravel, 1.5 m to bottom of exposure at 2.0 m, fine gravel and sand. Several large dead roots resembling those of feltleaf willow were found at 1.1 m. The surface soil showed the layer of matted roots and peaty organic matter characteristic of the wet tundra soils (Tedrow & Hill 1954, Tedrow, *et al.* 1957).

The most poorly drained sites along the transect have 2 to 8 cm

of standing water with a heavy cover of *Carex aquatilis* and *Potentilla palustris* together with *Sphagnum* sp. and *Aulacomnium palustre*. Shrubs are present on low mounds a few centimeters above the water level. *Salix pulchra* is most frequent but total shrub cover on these wet areas is low.

Around the edges of the areas with standing water, on very slightly higher ground, the moss cover seems to form small hummocks in the *Carex aquatilis* cover. The important bryophytes are *Hylocomnium alaskanum*, *Aulacomnium turgidum*, *A. palustre*, *Dicranum elongatum* and *Tomenthypnum nitens* (Hedw.) Loeske. On these low hummocks occur shrubs of alder and greenleaf willows about 0.5 m tall. *Vaccinium uliginosum*, *V. vitis-idaea* ssp. *minus*, *Ledum palustre* ssp. *decumbens*, and *Rubus chamaemorus* may contribute some cover around the base of these larger shrubs.

On still higher ground, often less than 30 cm above standing water, are found various combinations of species. In some sites, under the scattered low alder, the contribution of *Vaccinium uliginosum* is quite high and intermixed with it are small amounts of *Ledum palustre* ssp. *decumbens*, and occasionally *Betula nana* ssp. *exilis*. *Carex aquatilis* drops out and small amounts of *C. bigelowii* and *Eriophorum vaginatum* ssp. *spissum* occur. A heavy cover of the above group of mosses occurs along with the lichen *Peltigera aphthosa*. In other sites, the cover of alder may approach 60 per cent and the shrubs may reach over 1 m in height. The cover of *Vaccinium uliginosum* is somewhat reduced in these areas but otherwise the lower vegetation is like the preceding. A third combination, usually found on higher spots, shows a lower, more open alder-willow shrub with a greater contribution of *Carex bigelowii* and *Eriophorum vaginatum* ssp. *spissum*, together with the occurrence of *Empetrum nigrum*, *Lupinus arcticus* and *Vaccinium vitis-idaea* ssp. *minus*. On these sites the lichens *Cetraria cucullata* and *Cladonia* sp. may be important.

The preceding arrangement, in order of improving soil drainage of the terrace vegetation types, suggests a successional sequence in flat or concave areas. Careful examination of the location of reproduction of some species tends to corroborate this. It is probable that, with improving soil drainage, vegetation changes approaching this sequence would occur. However, on some areas of the young terrace, the sere would start on convex surfaces and thus the steps would be quite different, probably with grasses, lichens, drier mosses and willow shrubs characterizing the earlier stages. On some sites, it is obvious that peat accumulation and frost fissuring have resulted in a deterioration of drainage; this would probably initiate a sequence of vegetation change roughly the reverse of the first case. Numerous observations of dead plants in local wet spots indicate that these "retrogressions" do occur.

Along this lower terrace in areas outside the transect, other vegetation types occur. Stands of low greenleaf willow with an open understory of grasses, lupine and other forbs are found where sloping sandy gravel is at the surface. On convexities, where nearly sandless gravels are at the surface, a continuous but very low cover of dwarf heaths, dry mosses and lichens is present; this type may be referred to as dry meadow. Where peat has accumulated, as in abandoned meander scars, sedge marsh occurs (fig. 5). Wet tundra-meadows with various mixtures of *Eriophorum vaginatum* ssp. *spissum*, *Carex bigelowii*, dwarf heaths, mesophytic mosses and lichens occur



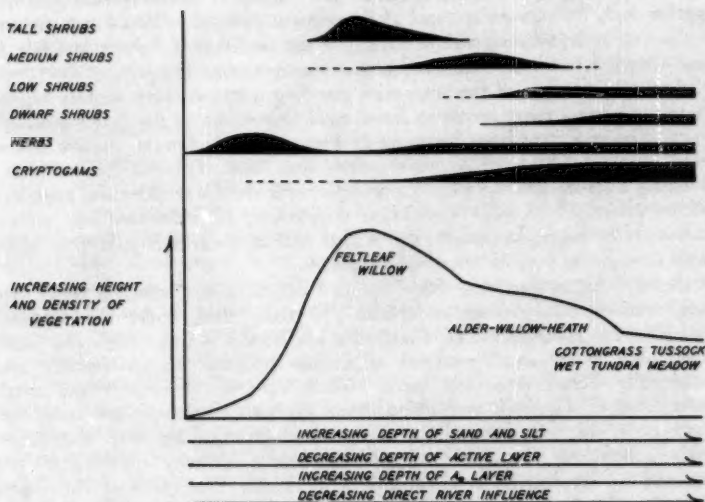


Fig. 6.—Generalized summary of the relative importance of the various vegetation types in the successful sequence as related to several edaphic factors.

on sites intermediate in drainage condition between marsh and the low willow shrub or dwarf heath dry meadow noted above. The soil materials associated with these wet tundra-meadow types on this terrace are mostly peaty, sandy silts or peaty, silty sands.

Although the transition between the vegetation mosaics of the lower terrace and the decadent feltleaf willow was absent at the detailed study area, such transitions do occur at points where the sharp break between lower terrace and floodplain is absent. In the few areas where such transitions were observed, the feltleaf willow clumps continued to decrease in height toward the terrace elevation. The presence of many dead stems of this species is characteristic in such areas. The greenleaf willows become more prominent and may range in height from 0.5 to 1 m. Associated with this is an increase in the importance of *Carex bigelowii*, *Arctagrostis latifolia*, *Vaccinium uliginosum*, *V. vitis-idaea* ssp. *minus* and frequently an increase in *Lupinus arcticus*. The bryophyte-lichen layer becomes more prominent and richer floristically (fig. 6). Where the gravels lack a mantle of sand and silt the vegetation will remain as low willow, with an increase in lichens, drier site mosses and dwarf heaths. The transition zone gives way to the terrace types described above.

#### VARIATIONS IN ALLUVIAL VEGETATION PATTERNS ON THE ARCTIC SLOPE

The alluvial vegetation pattern described above for a large meander on the Colville River at Umiat, Alaska, appears to be representative of that

found on similar sites along the larger rivers in the central part of the Foothills Province of the Arctic Slope. In other types of alluvial situations or in similar situations elsewhere on the Arctic Slope, patterns that differ in various ways occur. Several generalizations can be made concerning differences observed in alluvial vegetation at a number of locations in the region.

In the warmer (Conover 1956), central part of the Foothills Province in which Umiat is located, *Salix alaxensis* dominates a broader zone and the individuals are taller than in the cooler regions toward the coast or at greater elevations near the mountains. Furthermore, within the same general area the feltleaf willow zone is broader on gravelly alluvium than on sandy or silty materials. Since both a cooler summer and finer-textured alluvium characterize the alluvial areas in the western half of the outer Arctic Coastal Plain, the feltleaf willow zone is unimportant or even absent. Also, along several glaciated river valleys that have relatively low gradients at the mountain front (e.g., Killik River), sandy alluvium occurs. Although feltleaf willow may be present, it does not form extensive stands in such areas. In the eastern part of the Arctic Slope of Alaska, the alluvium is coarse even at the coast. Here, although feltleaf willow extends nearer the coast than in the western part, it rarely exceeds a few feet in height and does not occupy a broad zone. Spetzman (1951) indicates that this willow occurs on the Arctic Slope up to an elevation of 3,900 feet. However, observations made during the present study suggest that its contribution to alluvial vegetation is markedly reduced at elevations above approximately 2,000 feet.

Another variation in alluvial pattern from that described at Umiat is the presence of small stands of *Populus tremuloides* along streams near the mountain front in the eastern half of the Arctic Slope. These stands have not been examined on the ground but where observed from the air and on aerial photos they appear to occur in the older parts of the feltleaf willow stands. Spetzman (1951) indicates that this species is restricted to the floodplain of major rivers along the mountain front and that the largest known trees (15 to 30 cm diam. and 9 m tall) occur on alluvial fans in river valleys in the eastern part of the Arctic Slope. While the total area of these stands is small, the fact that they are the only stands of trees north of the Brooks Range in Alaska increases their importance. Meteorological data for the region are very sparse (Spetzman 1951, Conover 1956) and at present are not helpful in understanding the downstream or northern limits of the stands.

The width, height and species composition of the alluvial low shrub vegetation also varies considerably over the Arctic Slope. Height of shrub growth decreases at higher elevations and near the coast. However, low willows may occur along rivers all the way to the coast, being more conspicuous in the coarser alluvium and areas of greater relief on the eastern half of the Arctic Slope. On the lower reaches of some rivers, particularly in the western half, alluvial pioneer grasses and herbs frequently give way to marsh or meadow vegetation with scarcely a shrub zone expressed. The omission of a low shrub zone from the pattern is less common at higher elevations, although in certain very narrow V-shaped valleys the vegetation of the uplands may extend to the stream channel. Alder (*Alnus crispa*) is

absent from the floodplains and terraces near the coast and at higher elevations. In all probability there are other species restricted from these areas as well.

The pioneer vegetation also shows differences in species composition, abundance and growth-form over the Arctic Slope. In the absence of adequate study, the only generalization warranted is that the number of species decreases both toward the coast and at higher elevations. The reduction in number of pioneer species at elevations as high as 3,500 feet is probably not as marked as the reduction along the coast, particularly at the river mouths between the Colville and Kuk Rivers.

#### DISCUSSION

The vegetation zonation associated with stream sides is one of the more conspicuous features in the tundra region of northern Alaska. The regional vegetation is characteristically tussock or dwarf shrub meadow, marsh, lichen-moss-herb barrens or low shrub. Thus the stands of taller shrubs or (very locally) of small trees that make up a part of the alluvial zonation, are more conspicuous than their small total area would suggest. The perennial herb stands located between the tall shrub vegetation and the stream channel, though more nearly the same in life-form as the adjacent tundra, nevertheless have a composition and structure unrelated to the latter. That both of these alluvial vegetations are successional is obvious from their location along streams and from the changes that apparently take place in older stands left by migrating stream meanders.

While some aspects of arctic alluvial succession are unique, these alluvial habitats, vegetations and floras have much in common with those in similar sites outside the tundra zone. Some of the habitat conditions widely encountered on flood plains include periodic flooding, fluctuating water table, absence of surface organic layer, periodic erosion and deposition, light-textured soil materials of moderate nutrient content, and in some regions, ice abrasion. Outside the tundra region, taller vegetation along streams has been described in grassland (Kerner 1863, Moss 1955), in savanna (Beard 1955) and in desert (Billings 1951). These stands are usually attributed to improved water supply but Beard (1955) points out that other causes such as better soil drainage in alluvial areas may also be important. The strong floristic ties between arctic alluvial sites and those south of tree line also suggest that the former are not necessarily unique.

In biotic successions, two rather different causes of change have been recognized, *i.e.*, physical vs. biotic (Allee, *et al.* 1949), or allogenic vs. autogenic (Tansley 1935). The distinction is based upon whether seral changes progress primarily as a result of erosion, deposition and related physical processes, or whether they progress primarily as a result of such biotic phenomena as accumulation of organic matter, shade etc. Tansley (1935) says that such a distinction cannot be made with any degree of sharpness and that the terms allogenic and autogenic ought to apply to the factors rather than the entire sere. Dansereau (1954) in discussing vegetation change on Bray Island suggests that "allogenic stages are certainly less clearly related than autogenic ones."

In the succession occurring on the slip-off slope of the migrating meander, both allogenic and autogenic processes are operative (fig. 6). In the early stages near the stream channel, changes are due primarily to allogenic factors. Thus, increase in sedimentation, reduction in the depth, frequency, and duration of flooding, reduction in erosion, and related changes are allogenic, although the presence of plants may accelerate or retard these changes. In the later stages, autogenic factors predominate but are accompanied by allogenic factors, e.g., the depth to which the soil thaws is influenced by the insulating properties of the living vegetation layer and by the nature of the litter accumulation. It is also influenced by physical factors such as accumulation of finer sediments over the gravel and the effects of flooding in early removal of snow cover, soil heating and in flushing away accumulated litter. Depth of thaw in turn influences the moisture, aeration, temperature and mineral nutrients of the soil. Thus, different points along the transect from the stream channel to the terrace are characterized by different environments and these various environments are changing at different rates. The nature of the vegetation and its rate of change also differ along the transect. As one would expect, it is the higher or later stages of succession, those in which autogenic processes predominate, where the uniquely arctic characteristics occur. However, these later stages as well as the upland tundra are subject to physical (allogenic) processes essentially unique to permafrost regions, e.g., frost cracking, solifluction and thaw-collapse.

Observations indicate that the species common to the terraces, most of which also range over the uplands beyond the river valleys, are absent from the perennial herb and young feltleaf willow stands. *Lupinus arcticus* is a notable exception, being found commonly on floodplains, river terraces and in the foothills on steep slopes and crests. *Salix glauca* ssp. *desertorum*, *S. arbusculoides* and *Alnus crispa* which occur in very small numbers in the young feltleaf willow stands (see table 1) also occur away from the river valleys. This exclusion of most upland species from the younger floodplain is a widespread phenomenon not restricted to tundra regions. Of particular significance is the absence of moss, lichen, dwarf shrub and most sedge components of the upland. The environment of the floodplain obviously exceeds the tolerance ranges of each of these species in one or more ways. A few of the more obvious differences are: 1) direct effects of periodic flooding on plants, 2) inability to tolerate sedimentation, 3) periodic drought of surface soil and 4) absence of surficial organic layer and its microflora and fauna. These or other features of the environment might be particularly unfavorable to the germination and early development of the terrace species. That it is more than this is demonstrated by the failure of most terrace species to expand out from or even to continue to exist in the mats of terrace soil and vegetation that are deposited on the bars during highwater each year. The shallowness of the root or rhizoid systems of many of the terrace species, while a useful adaptation for the shallowly thawed terrace and upland soils, would prove less efficient in anchoring against flood waters and in reaching moisture when the sandy surface becomes dry.

While most of the terrace and upland species are more-or-less completely restricted from the floodplains, floodplain species are not entirely absent from the uplands. Many of these grasses and perennial herbs commonly occur on

deeply-thawed, bare, mineral soil or rubbly exposures on steep slopes some distance from floodplains (Spetzman 1951, Churchill 1955, Bliss 1956). Other species such as *Crepis nana* are less commonly found off the floodplain. Almost all of the floodplain species have deep root systems and can grow well in sites that are deeply thawed and become fairly dry in the surficial layers. Most do not grow on sites where dense upland vegetation occurs. These latter sites are characteristically shallowly thawed and usually have organic surface soils which are very near saturation. The fact that a thick organic mat and saturated soils are absent from almost all sites where these species are found is probably of some nutritional or microbiological significance in addition to the plant-soil water implications. In spite of the absence of complete fidelity to alluvial situations of all floodplain species, entire assemblages of these species are not found in non-alluvial situations.

Thus, in terms of the total change, arctic alluvial successions are characterized predominantly by what Egler (1954) has termed "relay floristics," in which the environment of the initial end of the sere, the floodplain, is completely restrictive to the species characterizing the other end. With time, predominantly allogenic and later predominantly autogenic processes operate both to eliminate the floodplain species and to permit the establishment of the terrace and upland species. The gradient across which this replacement occurs can be steep or gradual, depending upon texture of the alluvium, rate of meander migration, size of the stream, latitude and altitude.

The concepts of productivity, biomass and standing crop have been of considerable value in picturing successions (Lindeman 1942, Allee, *et al.* 1949, Odum & Pinkerton 1955). While it is unsound to consider only the green plant or producer part of the total community, comparisons of this part of the community for the various stages of the succession are of interest. The data obtained in the present study do not permit calculations of this type since they are expressions of per cent cover, height, and basal areas rather than weights. However, the general trend is probably one of increasing standing crop starting with the herbaceous communities and continuing into the young feltleaf willow stands. From the young feltleaf willow stands on through the old feltleaf willow to the various meadow, marsh and shrub tundra types, there appears to be a slight to sharp decline in standing crop depending upon the end type (fig. 6). However, in all except the driest sites there is an accumulation of surface organic matter which might equal or exceed the difference in standing crop between the terrace types and the young feltleaf willow type.

An understanding of the relative productivity for each community through an estimation of standing crop, however, is difficult, for a considerable portion of the standing biomass in all the shrub communities consists of perennial wood. However there is a greater accumulation of wood in the young feltleaf willow stands than in the other shrub community types. Information concerning longevity of the various shrub species would contribute valuable information which if combined with growth rate determinations for the same species (Bliss 1956) would aid in a more accurate estimation of annual production per unit area.

Odum and Pinkerton (1955) suggest that successions should show a continuous rise in biomass reaching a peak at the climax state. This is, of



course, predicated on the assumption that the potential productivity of the site does not change with the developing succession, *i.e.*, that the site does not deteriorate. Migrating stream meanders in desert regions would result in the gradual removal of additional water supplies. Galeria forest would be replaced by a desert shrub of considerably lower biomass. Thus, this primarily allogenic succession results in a deterioration of site or a reduction in potential productivity. Whittaker (1953:47) in reviewing the literature on succession and retrogression points out that Lüdi and Del Villar recognized both the generalization that biomass tends to increase during a sere and that there are exceptions to the generalization. The desert alluvial succession seems to be a clear example of an exception. The succession described above for the arctic tundra and that described by Drury (1956) for the sub-arctic are probably also exceptions. Further study directed specifically at this question would be most interesting.

#### SUMMARY

During the summer of 1953, a detailed study was made of the alluvial vegetation along the Colville River at Umiat on the Arctic Slope of Alaska. This vegetation may be arbitrarily divided into four communities: 1) a pioneer stage characterized by perennial herbs, 2) a vigorous willow stage dominated by the feltleaf willow *Salix alaxensis*, 3) a zone of deteriorating feltleaf willow with increasing cover of lower-statured greenleaf willows, mosses and herbs and 4) an alder-willow-heath type. These four communities can be considered as representing a successional series, arranged above from youngest to oldest and from stream channel to terrace across a migrating meander. The succession appears to take place as a result of both physical (allogenic) and biotic (autogenic) changes in the sites.

Each stage in the succession is associated with site conditions that differ from those characterizing the other stages. The very open pioneer herb community represents the colonization by a few perennial herbs of those bars which are exposed except during high water levels and over which the erosion force of the floodwaters is not too severe. Where the amount of sand and silt in and over the gravels is adequate, and where the impact of spring floods is not prohibitive, the perennial herb cover increases and fairly dense stands of *Artemisia* spp., *Lupinus arcticus*, other legumes, grasses, *Epilobium latifolium* and other forbs occur. These soils are mostly coarse-textured and deeply thawing. On the higher levels where the depth of sand is adequate, feltleaf willow may invade these perennial herb stands. The willow shrubs increase in height and density accompanied by a further increase in the density of the herb layer, the composition of which is essentially the same as that on the pioneer stands. The feltleaf willow stands are usually tallest and most vigorous near the transition to the pioneer herb communities. Sedimentation during floods continues in these stands and the mantle of silt and sand becomes thicker. The speed with which the soil thaws at the onset of the growing season is slower where the heavier ground cover provides better insulation, where the mantle of sand and silts is thicker and where the impact of spring flood waters is less. Within the willow stands, the tall feltleaf willow stems die and are replaced by low basal sprouts and other species of greenleaf willows. Associated with this deterioration of the tall

willows is an invasion of species which occur on the terraces above the floodplain. On the first terrace above the floodplain at Umiat, Alaska, the vegetation is a mosaic of greenleaf willow-alder shrub and cottongrass tussock-dwarf heath-Bigelow sedge-moss tundra meadow on the fine-textured soils, sedge marsh and ponds in the low areas and a xeric grass-greenleaf willow shrub or dwarf heath-lichen meadow on the coarse-textured raised areas. Depth of soil-thaw is much less on the terrace, largely as a result of increasing vegetation cover and accumulating peat. In the rolling uplands beyond the river valley, dwarf heath-cottongrass tussock wet tundra-meadow predominates on the silty, wet tundra soils.

An examination of alluvial vegetation along rivers elsewhere on the Arctic Slope suggests that the general relationships found at Umiat prevail over much of the central part of the region. However, northward nearer the Arctic coast the shrub zones are narrower and the shrub height is less. With increasing elevation, a decrease in shrub stature is found. In river valleys above 3,000 ft. to the south and west of Umiat, feltleaf willow stems are mostly less than 5 feet tall. Floristically, there is also a reduction in perennial herbs toward the mountains to the south and toward the Arctic Coast to the north.

These successional changes in community types are associated with site changes (see fig. 6). Associated with the community changes is an apparent increase in standing crop from the perennial herb communities through the young feltleaf willow stands. This is followed by a decrease from the old feltleaf willow stands through the mosaic of community types on the terrace. This apparent reduction in productivity during the latter stages in succession is associated with site deterioration.

#### REFERENCES

- ALEKSANDROVA, V. D. 1937—Tundras of the right bank of the Popigai River. *Trudy Arkticheskogo Instituta, Leningrad* 63:181-207. (Translation)
- ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT 1949—Principles of animal ecology. W. B. Saunders Co., Phila.
- BAXTER, D. V. AND F. H. WADSWORTH 1939—Forest and fungus succession in the lower Yukon Valley. *Univ. of Mich. School of Forestry and Conservation Bull.* 9.
- BEARD, J. S. 1955—A note on gallery forests. *Ecology* 36:339.
- BENNINGHOFF, W. S. 1952—Interaction of vegetation and soil frost phenomena. *Arctic* 5:34-44.
- BILLINGS, W. D. 1951—Vegetation zonation in the great basin of western North America. *Extrait des C. R. du Colloque sur Les bases écologiques de la régénération de la végétation des zones arides. U.I.S.B.* pp. 101-122.
- BLISS, L. C. 1956—A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecol. Monog.* 26:303-337.
- CANTLON, J. E. AND F. H. BORMANN 1953—Unpublished data.
- CHURCHILL, E. D. 1955—Phytosociological and environmental characteristics of plant communities in the Umiat region of Alaska. *Ecology* 36:606-627.
- CONOVER, J. H. 1956—Macro- and micro-climatology of the arctic slope of Alaska. Unpublished manuscript.
- CURTIS, J. T. 1947—The palo verde forest type near Gonivaves, Haiti, and its relation to the surrounding vegetation. *Carib. Forest* 8:1-26.
- DANSEREAU, P. 1954—Studies on central Baffin vegetation. I. Bray Island. *Vegetatio* 5:329-339.

- DRURY, W. H. 1956—Bog flats and physiographic processes in the upper Kuskokwim River region, Alaska. Contr. Gray herb. Harvard Univ. No. 178.
- EGLER, F. E. 1954—Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4:412-417.
- GORODKOV, B. N. 1944—Tundras of the Ob'-Yenisey divide. Parts I and II. *Sovetskaya botanika* 3, 4, and 5:3-31 (Translation).
- GROUT, A. J. 1940—List of mosses of North America north of Mexico. *Bryologist* 43:117-131.
- GRIGGS, ROBERT F. 1936—The vegetation of the Katmai District. *Ecology* 17:380-417.
- HALE, JR., M. E. AND W. L. CULBERSON 1956—A checklist of the lichens of the United States, Canada and Alaska. *Castanea* 21:73-105.
- HANSON, HERBERT C. 1951—Characteristics of some grassland, marsh, and other plant communities in western Alaska. *Ecol. Monog.* 21:317-78.
- 1953—Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. *Ecology* 34:111-140.
- HOPKINS, D. M. AND R. S. SIGAFOOS 1950—Frost action and vegetation patterns on Seward Peninsula, Alaska. U. S. Geol. Surv. Bull. 974-C:51-100.
- HULTÉN, ERIC 1949-1950—Flora of Alaska and Yukon, Parts I-X. *Lunde Universitets Arsskrift*, N.F., Vol. 37-46.
- KERNER, ANTON 1863—The plant life of the Danube Basin (From translation by Henry S. Conard, 1951. The background of plant ecology. Iowa State Coll. Press, Ames).
- LINDEMAN, R. L. 1942—The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.
- MAXWELL, JAMES 1954—Shallow seismic surveying in the permanently frozen ground of northern Alaska. Boston Univ. Phys. Res. Lab. Unpublished manuscript.
- MOSS, E. H. 1955—The vegetation of Alberta. *Bot. Rev.* 21(9):493-567.
- ODUM, H. T. AND R. C. PINKERTON 1955—Time's speed regulator. *Amer. Sci.* 43: 331-343.
- POLUNIN, NICHOLAS 1936—Plant succession in Norwegian Lapland. *J. Ecol.* 24:372-391.
- PORSILD, A. E. 1951—Botany of southeastern Yukon adjacent to the Canol Road. *Nat. Mus. Canad. Bull.* No. 121. Ottawa, Canada.
- RAUP, H. M. 1935—Botanical investigations in the Wood Buffalo Park. *Nat. Mus. Canad. Bull.* 74.
- SHELDIAKOVA, V. A. 1938—The vegetation of the Indigirka River basin. *Sovetskaya botanika* 4 and 5:42-79. (Translation)
- SOCHAVA, V. B. 1933—Tundras of the Anabara River basin. *Izvestiia Gosudarstvennogo geograficheskogo obshchestva* 65:340-364.
- SPEZMAN, L. A. 1951—Plant geography and ecology of the arctic slope of Alaska. Master's thesis. Univ. of Minn.
- TANSLEY, A. G. 1935—The use and abuse of vegetation concepts and terms. *Ecology* 16:284-307.
- TEDROW, J. C. F. AND D. E. HILL 1954—Soil characteristics of the arctic slope of Alaska, a pedologic report. Boston Univ. Phys. Res. Lab. Unpublished manuscript.
- , D. E. HILL, AND L. A. DOUGLAS 1957—Major genetic soils of the arctic slope of Alaska. *J. Soil Sci.* (in press).
- VASILEV, V. N. 1936—Reindeer pastures of the Anadyr District. *Trudy Arkhticheskogo Instituta, Leningrad* 62:9-104. (Partial translation)
- WHITTAKER, R. H. 1953—A consideration of climax theory: the climax as a population and pattern. *Ecol. Monog.* 23:41-78.

## A Revision of the Genus *Alisma* (Dill.) L.<sup>1</sup>

Albert J. Hendricks

Southern Illinois University, Carbondale

The genus *Alisma* (Dill.) L. consists of a plexus of taxa which have been placed, in most phylogenetic schemes, among the "primitive" monocotyledonous plants. Because of this the genus has long been of special interest to botanists. It has been monographed by Micheli (1881), Buchenau (1903), and Samuelsson (1932). However, none of these works has included an adequate study of the North American populations of the genus.

Lunell (1907, 1908, 1915) described a number of specific and infra-specific North American taxa of *Alisma*, but his diagnoses were often based on modifications induced by the environment. Evidently, he did not give much consideration to the inherent range of variability of the characters used. Fernald (1946) discussed briefly the merits of separating one eastern North American taxon of *Alisma* from the European *Alisma plantago-aquatica* L. (sensu Samuelsson), but apparently did not make an extensive study of North American populations of the genus. This paper is based on data obtained from field study of *Alisma* plants from several midwestern states, and from examination of herbarium specimens of collections made in widely distributed areas throughout the North American continent, as well as in Eurasia.

The genus *Alisma* was selected as the subject for this study because its members have several characteristics that contribute to a systematic investigation. The included plants are herbaceous-perennial in habit, which makes the maintenance of parental stock easy and provides a means for early production of flowers every year. The compound-panicle inflorescence of the plants supplies an abundant amount of fruits for growth studies and for root-tip smears of seedlings. Roots may be grown from seed within a week if the seed-coats are broken artificially. The single genome ( $n = 7$ ) is small enough to make chromosome counts relatively simple.

The objectives of this revision are to delimit and portray the inter-relationships of the taxa within the genus *Alisma*, and to determine the valid name of each taxon included.

The published descriptions of species of *Alisma*, after obvious synonyms are removed, total thirty-six. With diagnoses at infra-specific levels included, the total number of *Alisma* taxa described in the literature exceeds one hundred. Many of these descriptions defining new taxa were based on single character expressions, or on characters that may be modified by the environment. In many cases these modifications were not recognized as such. For example, size of plants and leaf-shape were characters frequently used. In *Alisma*, as in many paludal groups of plants, both of these characters may be exhibited in a wide variety of patterns, which may be either inherent, or

<sup>1</sup> Portion of dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Nebraska.

due to modification. In this paper characters used in diagnosis have been observed as much as possible to determine their patterns and ranges of inherent variation. Many of the effects of the environment on each character have been noted. The consistent concurrence of several of the expressions of these characters form the basis of the diagnoses of the taxa. It is hoped that the combinations of character expressions used depict to some degree the homology of the germ plasm of the individuals included in the respective diagnoses.

#### SOURCE OF DIAGNOSTIC CHARACTERS

Evidence of inter-relationship of taxa is found in virtually every field of botany by modern-day taxonomists. The evaluation of this data is usually obtained from statistical analysis. This study of *Alisma* plants includes information about their gross morphology, geographical distribution, serology, ecology, anatomy, and cytology.

Herbarium specimens provided the main source of material for study of the morphology of the *Alisma* plants, but morphologic characters obtained were checked in living populations whenever possible. The geographic origin of each herbarium specimen was recorded and the distribution of the entities ultimately determined were plotted as exactly as possible on maps. These distributions indicate the influences of latitude on the taxa. Among these the length of the growing season and the temperature of the ground (water) may be important influences in determining their migration patterns.

Plants from many of the populations observed in the field were transferred to the greenhouse and to an experimental pond in order to have some

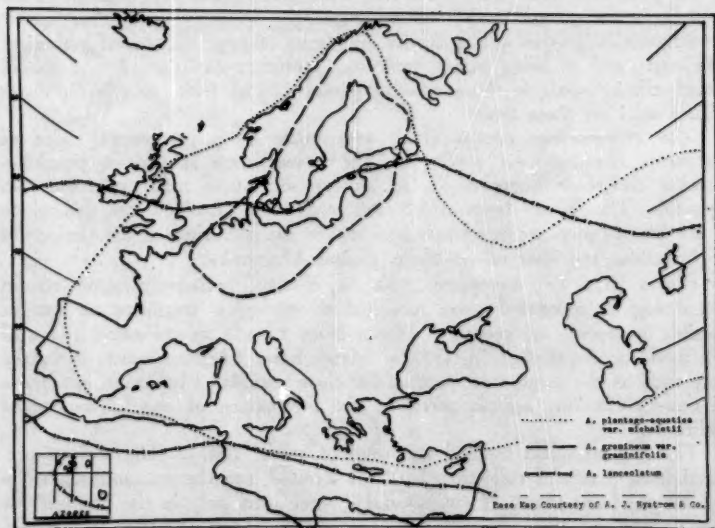


Fig. 1.—Boundaries of the distribution of three *Alisma* taxa in Europe.



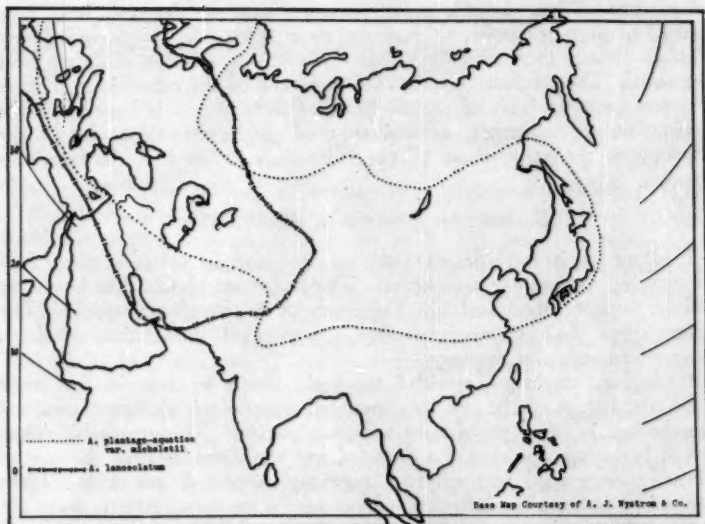


Fig. 2.—Boundaries of the distribution of two *Alisma* taxa in Eurasia.

check on environmental influences. Transplantings were made in all seasons of the year, and fruits from several of these populations were planted in the greenhouse for growth studies of seedlings.

Anatomical studies of the flowers and fruits of large samples of herbarium specimens, and of living plants, indicated significant variations in the size of guard cells in sepals, in the number of dorsal sulci on fruits, and in the depth of the sulci on these fruits.

The chromosome counts cited were made from permanent slides of meristems from *Alisma* seedlings. The tissues were stained in propionocarmine and were immersed in an alcohol series and made permanent in Euparal. The plants from which the seeds were obtained for this phase of the investigation are deposited specimens in the herbarium of the University of Nebraska and that of Southern Illinois University.

Plants from two sympatric taxa of *Alisma*, tentatively separated on morphological differences, were subjected to serological treatment to test for possible homology of proteins. Plants from Hendricks collection 111 and 112 made on September 26, 1952 at Marsh Lake, Cherry County, Nebraska were used as the sources of material for these entities. Herbarium specimens of these collections are deposited in the Herbarium of the University of Nebraska.

The ring-precipitin method was used (Chester, 1937). The antigen prepared from plants of collection 112, was injected into the test animals, while the antigen from plants of collection 111 were used only in the ring-test for titer against the 112 antisera. Also, as checks in the ring-test, antigens of plants from *Sagittaria* sp., *Echinodorus* sp., *Lophotocarpus* sp., and *Yucca*

sp. were prepared and tested in a manner similar to that for plants of collection 111.

Some homology of proteins in the two *Alisma* taxa was indicated by the formation of precipitin rings in the inter-phase between the test-animals' antisera and the antigen extracts, while the tests of the antigens of the other genera produced negative results. It is worth noting that the titers obtained for the two *Alisma* taxa indicated that while the two groups of plants certainly have some proteins in common, there are differences in other proteins between the two groups.

#### DISPOSITION OF THE GENUS

*Alisma* may have originated in the lowlands of central North America on the margin of the Washita Sea in the Early Cretaceous period when many angiosperms were probably becoming adapted to the aquatic environment (Axelrod, 1952). There is evidence of more than twenty-five monocotyledon families in the Cretaceous and Cenozoic deposits of North America. Included in this list is the family Alismataceae, which is represented in the lower Upper Cretaceous strata (Arnold, 1947).

As the climate was still warm in this period *Alisma* populations may have migrated north-east through Greenland to Europe, as well as westward to the Pacific coast, when the inland sea began to recede, and thence north to the Alaskan Peninsula. From Alaska they may have migrated into Siberia and southward into eastern Asia.

Seven taxa of *Alisma* have been delimited in this investigation. Several of these are recognized entities from the monographs of previous workers.

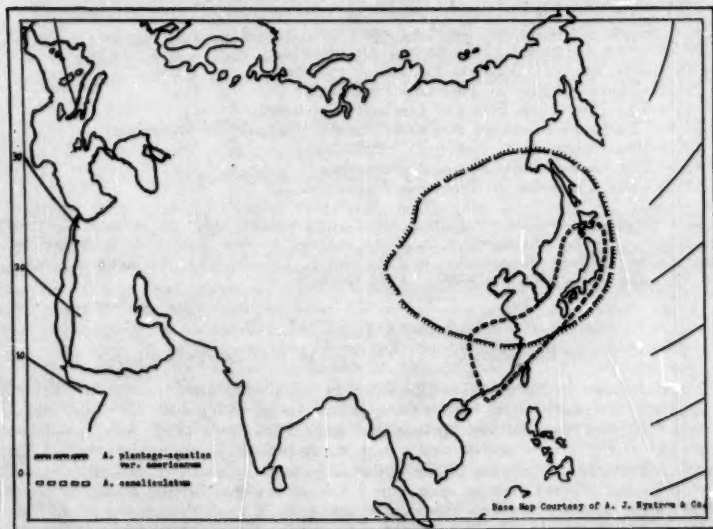


Fig. 3.—Boundaries of the distributions of two *Alisma* taxa in Asia.

One of these, *A. plantago-aquatica* L. var. *michaletii* (Aschers. & Graebner) Buchenau, is apparently ubiquitous in all temperate climates. Another, *A. gramineum* Gmel. var. *graminifolia* (Wahlenberg) comb. nov., is widely distributed in North America and Eurasia in sub-boreal latitudes.

In this revision inter-relationship of the sub-generic taxa is based on the premise that the most "primitive" taxon in the genus includes plants with the greatest number of characteristics held in common with plants of the other taxa in the genus. The conjecture is made that this "primitive" *Alisma* entity may be somewhat similar to the ancestral population of all of the plants in the group. On this basis *A. plantago-aquatica* var. *michaletii* seems to be the most primitive taxon.

It appears possible that *A. gramineum* var. *graminifolia* may have been the earliest of the derived taxa to separate from *A. plantago-aquatica* var. *michaletii*, when the latter was still highly heterozygous. Thus, both of these were flexible enough to become widespread. Perhaps the remainder of the taxa evolved from these two either as ecotypes or polyploids with sub-continental distributions.

#### HERBARIA

The herbarium specimens listed after each taxon diagnosis indicate the geographic range of individuals included. The total number of specimens examined is noted in parentheses before the herbarium specimen lists.

Over twenty-six hundred herbarium specimens were received and annotated. The plants were borrowed from these herbaria:

- CAN—The Herbarium of the National Museum of Canada.
- F—The Herbarium of the Chicago Museum of Natural History.
- GH—The Gray Herbarium of Harvard University.
- IND—The University of Indiana Herbarium.
- MIN—The University of Minnesota Herbarium.
- MO—The Missouri Botanical Gardens Herbarium.
- NEB—The University of Nebraska Herbarium.
- NY—The New York Botanical Gardens Herbarium.
- RM—The Rocky Mountain Herbarium, at the University of Wyoming.
- UC—The University of California Herbarium.
- US—The United States National Herbarium.
- WIS—The University of Wisconsin Herbarium.

The herbarium symbols are from a recent, international index of herbaria (Lanjouw and Stafleu, 1954). The co-operation of the curators at these institutions is appreciated. Also, thanks are herewith extended to Dr. John F. Davidson for his many suggestions and his counsel in the various phases of this study.

#### ALISMA (Dill.) L.

Species Plantarum 1:342.1753. (T.: *A. plantago-aquatica* L.)

Erect, scapose, herbaceous-perennials from an apically flattened corm with dormant lateral buds, and dorso-lateral fibrous roots; radical leaves arising from the upper surface of the corm, sheathing the inner petiole and scape bases, with forms from gramineous throughout to leaves with cordate lamina and sturdy petioles; scapes straight to undulate, emerging from the central area of the upper surface of the corm, leafless, with one to many bracteate, whorled verticils, each with 3-6 main branches bearing numerous umbel-like bracteate clusters of pedicels appearing to terminate in small flowers, the whole forming a compound panicle; calyx trimerous, herbaceous; corolla trimerous, petals white, rose-tipped, or rose; stamens six, included; pistils numerous, laterally flattened, in a single,

whorled ring on the flattened receptacle, unilocular, one-seeded, with styles sub-apical, ventral, tapered, curved and terminate-papillate.

Four species are included. *A. plantago-aquatica* L. is ubiquitous in temperate climates; *A. gramineum* Gmel. is widespread at sub-boreal latitudes in North America and Eurasia; *A. lanceolatum* With. has its center of distribution in southern Europe; and *A. canaliculatum* A. Braun & Bouche is found in Japan, and eastern Asia.

#### KEY TO THE SPECIES OF *ALISMA*

- I. Leaves lanceolate to ovate lanceolate. Sulci on mature fruits shallow (0.1 mm, or less), and with the fruits usually uni-sulcate. The main axes of secondary branches on the scapes are apparently indeterminate in their growth, and are further branched laterally. Angles between pedicels on umbels are small and most pedicels are erect ..... *Alisma plantago-aquatica*.
- I. Leaves weak and ribbon-like, linear, narrow-lanceolate or narrow-spatulate. The main axes of secondary branches on the scapes appear to terminate abruptly in an umbel, and branching is very limited ..... II
- II. Leaves narrow-spatulate with the widest portion of the long, narrow lamina near the distal end. Corollas are white. The single sulcus is more than .1 mm in depth on the dorso-apical surface of each mature fruit. Pedicels are usually erect and angles between them, on the same umbel, are small ..... *A. canaliculatum*.
- II. Leaves ribbon-like to narrow-lanceolate. Corollas deep-rose, or purple in color ..... III
- III. Leaves are narrow-lanceolate with the proximal ends of the lamina wider than the much attenuated distal ones. The dorso-apical surfaces of the mature fruits are uni- or bi-sulcate. The ratio of width to length in the leaf lamina is usually from 1/4 to 1/3. Scapes are slender but are usually erect ..... *A. lanceolatum*.
- III. Leaves are weak and ribbon-like, linear, or linear-lanceolate. The distal and proximal ends of the lamina, where these are present, are either equally obtuse or taper at a slightly more acute angle at the distal end. The ratio of width over length of leaf lamina ranges from 1/11 to 1/4. The dorso-apical surfaces of the mature fruits are bi-sulcate. Angles between the bases of pedicels within umbels are often large and the appearance of the whole umbel is characteristically lax. Scapes are sturdy and somewhat ligneous, but are often undulate to extremely contorted ..... *A. gramineum*.

#### *ALISMA PLANTAGO-AQUATICA* L.

Figs. 1-4

*A. plantago* Δ. L., Sp. Pl. 1:342. 1753.

Perennial; from a corm 1-4 cm or rarely more in diameter, the lateral and basal surfaces covered with coarse fibrous roots; leaves 5-60 cm long, 1-15 cm wide, arising from the upper surface of the corm, enveloping the inner petiole and scape bases; petiole sheaths often 15 mm wide at base, but tapering abruptly to 5-8 mm over most of their length; lamina lanceolate to ovate-lanceolate, 2-30 cm wide, expanding from the distal ends of the petiole; scapes 2-9 dm high, emerging from the central area of the upper surface of the corm, developing 3-9 scarious-bracted verticils, each with 3-6 main branches; panicle subspherical, up to 7 dm in diameter, much branched, the branches strongly indeterminate, but appearing to terminate in bracteate umbels of pedicels; pedicels 5-20 mm long, erect or strict; flowers with 3 herbaceous sepals subequalling the 3 evanescent, white, often purple-tipped petals; stamens 6; achenes 5-20 in a ring on a flattened receptacle, each with one or rarely two sulci less than 0.1 mm deep, on the dorso-apical surface; fruiting heads 2.5-7.0 mm in diameter.

*Type locality*.—In European waters. (T.: Linn. Herb. London, no. 473/1, photo!).  
*Type species for Alisma*.

*Distribution*.—Throughout Europe and Asia (figs. 1-3), but most common in temperate latitudes. It is also common in lands of the Mediterranean



Fig. 4.—Boundaries of the North American distribution of *Alisma plantago-aquatica* L.

coast-line, and in the coastland of eastern Africa. It is known in Australia and has been collected in South America. In North America it attains great latitudinal distribution, being common from the sub-tropical climate of Florida to the boreal forests of Canada (fig. 4).

*Discussion.*—The geographical distribution of this species is considerably greater than those of the remaining three species in the genus. It appears to be widespread around the world, and its borders over-lap those of each of the other species.



In the past the series of populations that comprise *A. plantago-aquatica* L. have often been described as species or sub-species. One of the outstanding features of this species, and indeed of the genus, is the remarkable uniformity of appearance of the plants.

Micheli (1881) had considered *A. plantago-aquatica* L. to be the predominant species in the genus with the plants being very uniform throughout in its characteristics.

Buchenau (1903) described only one variable species in the genus *Alisma*. This was *A. plantago (aquatica)* L., which he considered to be comprised of the varieties  $\alpha$  *michaletii*,  $\beta$  *arcuatum*, and  $\delta$  *parviflorum*. The varieties *michaletii* and *parviflorum* have been considered as valid in this present revision, except that the geographical distribution of the former has been increased to include its presence in North America and in western Asia. The description of the variety *arcuatum* places it in *A. gramineum*.

In addition to the varieties *michaletii* and *parviflorum*, a third variety—*americanum*—is recognized here.

Of the three varieties *michaletii* is the most widespread, being found in North and South America, Europe, Africa, Australia, and Asia. The variety *americanum* is found in North America and eastern Asia. The variety *parviflorum* is limited to the southeastern United States.

Cytological studies by the author, which demonstrated the diploid nature of the species ( $2n = 14$ ), are in agreement with the previous reports of Oleson (1941) and Erlandsson (1946). *A. triviale* Pursh, included in synonymy here, has a diploid number  $2n = 14$  according to some reports (Brown, 1946; and Baldwin & Speese, 1955). Also, rare tetraploid plants have been collected. These polyploids have been placed in the variety *americanum* on the basis of morphologic characters.

The results of a hybrid index based on data collected from a modified random mixture of *A. plantago-aquatica* and *A. gramineum* plants indicate that a condition of reduced introgressive hybridization exists between these two taxa. Despite this, the morphological characters that separate these two groups are usually well defined.

The results of the serology tests indicate that there exist some homologous proteins in the plants of this taxon and in those of *A. gramineum* Gmel. The tests also indicate certain differences in other proteins in the two groups.

#### KEY TO THE VARIETIES OF *ALISMA PLANTAGO-AQUATICA*

- A. The diameters of the rings of the mature fruits from individual flowers are 4.5 mm or more. Petals are white, but are often purple-tipped. Fruits are uni-sulcate or bi-sulcate ..... *Alisma plantago-aquatica* var. *michaletii*.
- AA. The diameters of the rings of the mature fruits from individual flowers are close to 4 mm. Petals are white. Fruits are uni-sulcate or bi-sulcate..... *A. plantago-aquatica* var. *americanum*.
- AAA. The diameters of the rings of mature fruits from individual flowers are 3.5 mm or less. Petals are white. Fruits are mostly uni-sulcate..... *A. plantago-aquatica* var. *parviflorum*.

#### *ALISMA PLANTAGO-AQUATICA* L. var. *MICHALETII* (Aschers. & Graebner) Buchenau 1903.

*A. plantago* Δ. L., Sp. Pl. 1:342. 1753. (in part).

*A. parnassifolium* Bassi 1768 ex Linn. Systema Naturae ed. 12, tome 3:230. 1768.

- A. latifolium* Gilbert, J. E. ex Flora Lithuania Inchoata II:222. 1781.  
*A. dubium* Willdenow ex Florae Berolinensis Prodrumus Secundum Systema Linneanum 1:132. 1787.  
*A. paniculatum* Stokes ex Botanical Materia Medica 2:334. 1812.  
*A. majus*, Gray, S. F. ex Nat. Arr. Brit. Pl. 2:216. 1821.  
*A. reniforme* Don, D. ex Prodrumus Flora Nepalensis 1:22. 1825.  
*A. plantagineum* St. Lager ex Annales Societe Botanique Lyons 7:119. 1880.  
*A. plantaginifolium* St. Lager ex Etud. des Fleurs, ed. 8, 2:821. 1889.  
*A. plantago-aquatica* L. ssp. *Michaletii*, Aschers. & Graebner ex Synops. Mitteleur. Flora 1:382. 1897.  
*A. Michaletii* Aschers. & Graebner ex Flora of Nordostdeuther Flachland: 65. 1898.  
*A. plantago (aquatica)* L. var. *a Michaletii*, Buchenau ex Die Pflanzenreich 16 (IV. 15):1-66. 1903.  
*A. superbum* Lunell ex Bull. Leeds Herbarium, No. 2:5. 1908.  
*A. superbum* Lunell, var. *angustissimum* Lunell ex Bull. Leeds Herbarium, No. 2:5. 1908.  
*A. superbum* Lunell, var. *lanceolatum* Lunell ex Bull. Leeds Herbarium, No. 2:5. 1908.  
*A. subcordatum* Raf. var. *superbum* Lunell ex American Midland Naturalist 4:164. 1915.  
*xA. rhinocarpum* Schotsman (= *A. lanceolatum* With. *xA. plantago-aquatica* L.) 1949.

The abaxial surfaces of the herbaceous sepals have guard cells that average 48.7 microns in length with a standard deviation of 4.7 microns; the petals are white, often with purple tips; the fruiting heads have diameters from 4.25-6.5 mm or more, and consist of fruits with mostly one sulcus on their dorco-apical surfaces, although many of the fruits in the corners of the triangular shaped heads have two sulci.

*Type locality*.—"Most plentiful in all communities." Germany. The Ascherson Herbarium at Berlin-Dahlem was destroyed in World War II. The authentic type-material was very likely in this collection.

*Distribution*.—The center of the distribution of this entity is in North America (fig. 4) but it is also ubiquitous in Europe (fig. 1); it has also been scantily collected in South America. In Europe it is found in every country, but is more prevalent in the more temperate latitudes. It is also widely distributed in the middle latitudes of Asia, as far east as Japan and as far north as Siberia (fig. 2).

In eastern and midwestern North America it is found from latitude 40° to 50°, and is thus somewhat restricted to the states and provinces on the border separating Canada and the United States. However, specimens have been collected as far south as latitude 37° in California and in southern Colorado.

*Discussion*.—Linnaeus' original description of *A. plantago-aquatica* in 1753 placed the taxon in Europe. He described the included plants as having acute-ovate leaves and obtuse, triangular fruits. He considered the plants to be widespread in Europe.

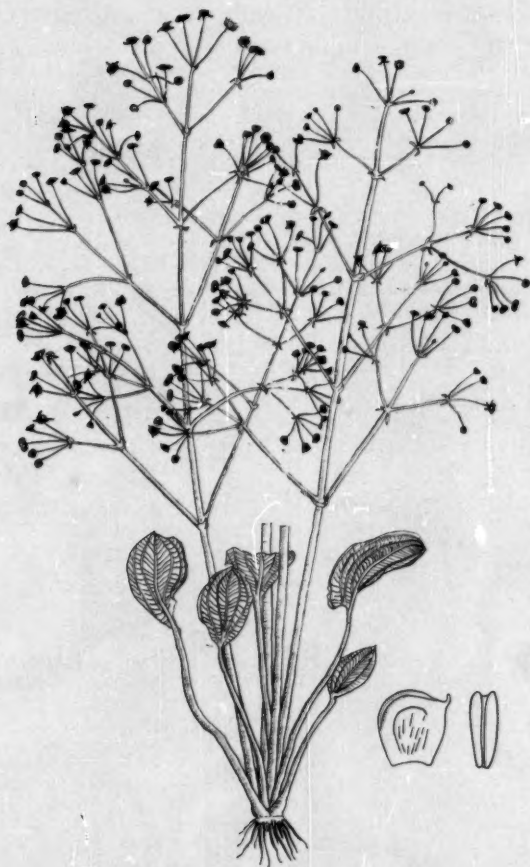


Fig. 5.—*Alisma plantago-aquatica* L. var. *michaletii* (Aschers. & Graebner) Buchenau 1903. Habit,  $\times 1/5$ ; achenes,  $\times 4$ .

This description was suitable until it was observed that there were at least two populations in the species that had, among other characters, leaves that were not acute-ovate in shape. These populations were not as widespread as that originally described by Linnaeus, but they resulted in the descriptions of several sub-specific taxa.

Ascherson and Graebner (1897) described a subspecies of *Alisma* in Europe with heart-shaped, somewhat rounded leaves. They designated this as *A. plantago-aquatica* ssp. *michaletii*.

Buchenau (1903) reduced Ascherson's and Graebner's sub-species to the variety *a. michaletii*.

Samuelsson (1932) considered this same European taxon with acute-tipped, rounded leaves to be the true *A. plantago-aquatica* L. (sensu Samuelsson). This same European taxon has been included in the present analysis in *A. plantago-aquatica* var. *michaletii*.

There is some evidence for the existence of reduced introgressive hybridization between this variety and *A. gramineum* Gmelin. In Europe the large over-lapping of the distribution of this variety with that of the geographically limited *A. lanceolatum* With. suggests that the variety *michaletii* may have given rise to *A. lanceolatum*.

Large increases in length of the guard cells have been frequently used as indicators of polyploidy (Cain, 1944). The lengths of sepal guard cells in plants of this group are about eighty-three percent of the tetraploids' guard cell lengths found in *A. canaliculatum* A. Braun & Bouche.

*Specimens examined* (total: 521).—United States. WASHINGTON: Pullman, J. E. Weaver, July 1914 (NEB); Pullman, W. R. Hull n. 629 (F); Hageman, F. H. Lamb n. 1280 (F). OREGON: The Dalles, J. W. Thompson n. 11893 (MO). CALIFORNIA: Palo Alto, E. L. Greene n. 3342 (F). IDAHO: Nampa, Canyon Co., A. Nelson & J. F. Macbride n. 1066 (F). ARIZONA: Near Flagstaff, Herbert C. Hanson n. A.897 (NEB). COLORADO: Fort Collins, C. J. Crandall n. 2518 (NEB, F); Boulder, R. J. Pool 7/3/07 (NEB). SOUTH DAKOTA: Brookings, A. G. Johnson 9/5/03 (MO); Artas, L. A. Hanna 6/8/29 (MO). NORTH DAKOTA: Leeds, J. Lunell, 7/20/09 (MO); Pembina, H. F. Bergman n. 2076 (MO). MINNESOTA: Lake Kabetogama near Arrowhead Lodge, St. Louis Co., Olga Lakela n. 9418 (MIN.) WISCONSIN: Along road, Reesville, J. W. Rhodes n. 456 (WIS). NEBRASKA: Sheridan Co., near Ellsworth, Flora Sandoz n. 370 (NEB); Kennedy, J. M. Bates n. 6746 (NEB); Grant Co., 3 miles northeast of Whitman, P. A. Rydberg n. 1616 (NEB); Cherry Co., J. G. Smith & Roscoe Pound n. 233 (NEB); Merrick Co., 6 miles east of Central City, Fred Eastman 8/6/03 (NEB). MISSOURI: Melugen, E. J. Palmer n. 3786 (MO). IOWA: Clayton Co. at Marquette, W. L. Tolstead 8/31/33 (NEB). INDIANA: Notre Dame, J. A. Nieuwland n. 11335 (MO). NEW YORK: Between Irvington & Tarrytown, J. H. Barnhard n. 329 (NY). MASSACHUSETTS: Martha's Vineyard, Haven, C. C. Curtiss 8/30/92, F. J. R. Churchill Cheshire 8/17/15 (MO). MAINE: Peak's Island, H. J. Scoggan n. 25 (CAN); Shore of Chemo Pond, Bradley, O. W. Knight 7/29/05 (RM).

Canada. BRITISH COLUMBIA: Chilliwack Valley, J. M. Macoun n. 26,821 (F). SASKATCHEWAN: North of Prince Albert, J. Macoun n. 14004, 14005 (CAN); H. M. Raup n. 1122 (CAN); and J. Macoun & Herriot n. 76885 (CAN). QUEBEC: Longueuil, near Montreal, Fr. Marie-Victorin n. 20410 (MO). NOVA SCOTIA: Kingsport, Howe & Lang n. 331 (NY); Grand Pre, Howe & Lang n. 378 (NY).

Europe. FRANCE: Royan, A. Guillon 8/2/90 (NEB); Doullens (Somme), C. Copineau 7/26/87 (US). GERMANY: Berlin, T. S. Brandegee 1870; Thuringia, Reinach 7/22/01; J. M. Greenman 7/12/00; O. Lügner 10/8/79. ENGLAND: A. E. Lomax 8/10/92; T. W. Edmondson n. 175. RUSSIA: Myherinkh, Froshkraut n. 122; A. Tauhtadschen n. 281. SWEDEN: J. Lunell 7/27/97; Ivar Tidestrom 7/15/94; and C. Srottsberg 4/28/93.

Asia. PUNJAB: Near Rawalpindi, R. R. Stewart n. 13817 (NY, US). SIBERIA: A. Krystofovic 1910. CHINA: C. Schneider n. 2697.

Africa. BRITISH EAST AFRICA: Vic. Saba-Saba, C. E. Mearns n. 1171 (NY, US). TUNISIA: M. Gandoger. ABYSSINIA: Schimper n. 411538.

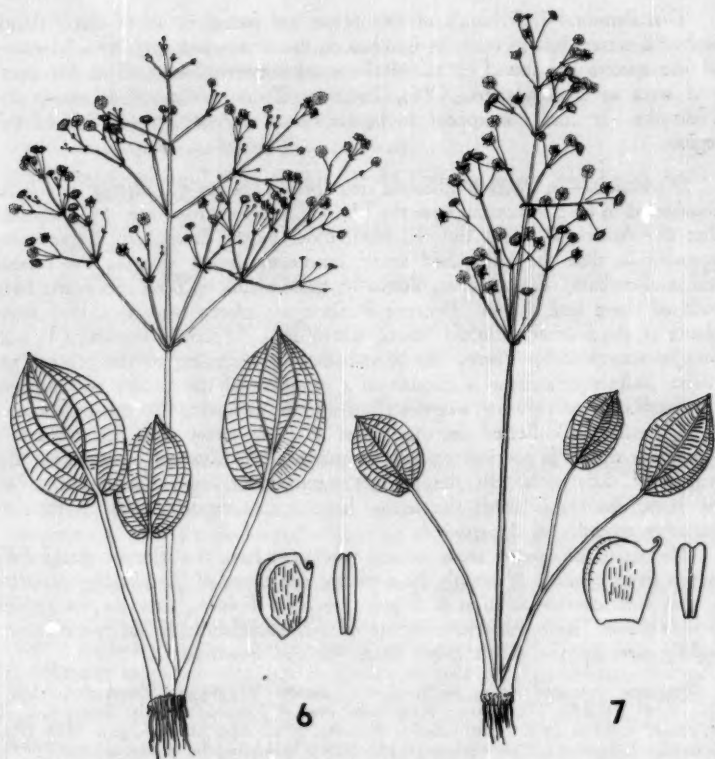
#### ALISMA PLANTAGO-AQUATICA L. var. PARVIFLORUM (Pursh) Torr. 1824.

*A. subcordatum* Rafinesque ex Med. Repos. New York 2:5. 1808.

*A. parviflorum* Pursh ex Flora Americae Septentrionalis 1:252. 1814.

*A. odoratum* Rafinesque ex Flora Ludovicana: 17. 1817.

*A. plantago* L. var. *parviflorum* (Pursh) Torr. ex Flora North & Mid. U. S. 1:382. 1824.



Figs. 6, 7.—6. *Alisma plantago-aquatica* L. var. *parviflorum* (Pursh) Torr. 1824. Habit,  $\times 1/5$ ; achenes,  $\times 4$ . 7. *Alisma plantago-aquatica* L. var. *americanum* J. A. Schultes & Schult. 1830. Habit,  $\times 1/5$ ; achenes,  $\times 4$ .

- A. plantago* L. var. *parviflorum* Franchet et Savatier ex Enum. Plant Japonia 2:16. 1876.  
*A. plantago* L. var. *Michaletii*, f. *stenophyllum* Aschers. & Graebner, ex Synops. Mitteleur Flora. Ed. I:383. 1898.  
*A. plantago-aquatica* L. var. *parviflorum* (Pursh) Farwell ex Ann. Rep. Comm. Parks & Boulev., Detroit xi:44. 1900.  
*A. subcordatum* Rafinesque var. *stenophyllum* (Aschers. & Graebner). Lunell ex Am. Midland Nat. 4:164. 1915.  
*A. plantago* L. var. *parviflorum*, f. *latifolium* Lunell ex Bot. Gaz. 43:210. 1907.

The abaxial surfaces of the herbaceous sepals have guard cells that average 38 microns in length with a standard deviation of 1.06 microns; the petals are white; the fruiting heads have diameters that do not exceed 3.74 mm and consists of fruits each of which has on its dorso-apical surface usually a single sulcus.

*Type locality*.—The forests of New Jersey and Pennsylvania. Pursh.



*Distribution.*—Individuals of this taxon are found in all of the Atlantic seaboard states, but increase in number to the southward (fig. 4). Members of the species are found in all of the southeastern states, and as far north and west as Pennsylvania, Ohio, Indiana, Illinois, Missouri, Kansas, and Nebraska. It does not appear to be native to any habitats outside of this region.

*Discussion.*—In 1808 Rafinesque described a species of *Alisma*, which he considered to be common all over the United States at that time. He indicated that the American plants differed from those in the European *A. plantago-aquatica* in that the latter had acute, lanceolate leaves whereas the former had semi-cordate, obtuse leaves. Actually, these plants on both continents have both of these leaf shapes. Because Rafinesque's plants were described from plants of the southern United States, where only *A. plantago-aquatica* L. var. *parviflorum* (Pursh) Torrey has been collected, according to the present revision, Rafinesque's name is considered a synonym of the variety *parviflorum*.

Pursh's *A. parviflorum* was described by him as having "leaves and flowers small," and was collected on the "coast of New Jersey and Pennsylvania." He wrote that this species strongly resembled "*A. Plantago*" except for the mentioned differences. In the present arrangement, only the condition of the small flowers is used; the leaves have a size range similar to that in the other varieties of the species.

The sepals of flowers from mature specimens have the shortest guard cells in the entire genus. Although these plants and those of *A. plantago-aquatica* L. var. *americanum* Schultes & Schult. are both diploids, they do not appear to hybridize. The northwestern limits of the distribution of var. *parviflorum* slightly over-lap the southeastern limits of var. *americanum*.

*Specimens examined* (total: 303).—United States. VERMONT: Manchester, M. A. Day n. 415 (GH). DELAWARE: Four miles west of Rehoboth Beach, Sussex Co., R. McVaugh n. 6548 (F). NEW JERSEY: Camden, J. C. Martindale August 1875 (F). GEORGIA: Lafayette, R. M. Harper n. 190 (US); Lafayette, P. Wilson n. 190 (NY). VIRGINIA: Prince Edward Co., J. D. Smith 8/23/80 (US); Foot of Signal Knob, Massanutler Mts., H. Allard n. 2138 (US, NY); northeast shore of Little Gunpowder River, one-third mile from the mouth, G. H. Shull n. 310 (NY). NORTH CAROLINA: Nashville, R. K. Godfrey n. 5156 (US). PENNSYLVANIA: Chester Co., J. T. Rothrock 7/18/82 (F); vicinity of Reinholdsville, J. K. Small 8/26/89 (F); Dillerville Swamp, Lancaster Co., A. A. Heller 7/10/01 (F). ILLINOIS: Herod, G. P. Churchill 7/30/98 (NEB). INDIANA: Swamp three miles southeast of Otis, R. M. Tryon n. 1568 (F). IOWA: Ringgold Co., M. F. L. Fitzpatrick 1898 (NY). NEBRASKA: Weeping Water, T. A. Williams, August 1888, and Itabash 7/22/89 (US). KANSAS: Pottawatomie Co., J. B. Norton n. 849 (GH, US). TEXAS: Canadien R., A. H. Howell n. 85 (US); Dallas, J. Reverchon n. 554 and 934 (GH). MISSOURI: Northwest of Chillicothe, S. Sparling n. 1049-B (F); Gasconade River, Lueleke Co., J. A. Steyermark n. 13908 (MO); Willow Springs, B. F. Bush 8/12/92 (MO). KENTUCKY: Warren Co., S. F. Price 7/4/98 (MO).

ALISMA PLANTAGO-AQUATICA L. var. AMERICANUM

J. A. Schultes & Schult. 1830.

Fig. 7

*A. plantago* sensu Michx. ex Fl. Bor.-Am. i:218. 1803. (not L. Syst. ed. 10, ii:993. 1759).

*A. flavum* Thunberg ex Flora of Japan 1:153. 1784.

- A. triviale* Pursh ex Pl. Am. Sept. i:252. 1814.
- A. plantago-aquatica* L. var. *americanum* J. A. Schultes & Schult. ex Carolia Linne Equitis Systema Vegetabilium 7, pt. 2:1598. 1830.
- A. plantago* L. var. *triviale* (Pursh) Britton, Sterns & Poggenberg, ex Prelim. Cat. N. Y. Pl. 58. 1888. (var. *americanum* Gray).
- A. brevipes* Greene ex Pittonia IV:158. 1900.
- A. plantago-aquatica* L. var. *triviale* (Pursh) Farwell ex Ann. Rep. Comm. Parks & Boulev. Detroit xi:44. 1900.
- A. plantago-aquatica* ssp. *brevipes* (Greene) Samuelsson ex Arkiv För Botanik 24A. n. 7:19. 1932.
- A. plantago-aquatica* L. ssp. *orientale* Samuelsson ex Arkiv För Botanik 24A. n. 7:19. 1932.
- A. orientale* (Samuelsson) Fuzepezuk, ex Fl. U.R.S.S. 1:281. 1934.
- A. plantago-aquatica* var. *brevipes* (Greene) Marie-Victorin ex Flore Laurentienne 615. 1935.
- A. plantago-aquatica* var. *brevipes* (Greene) Rouleau ex Nat. Canadien 71(11/12): 272. 1944.

The abaxial surfaces of the herbaceous sepals have guard cells that average 45.1 microns in length with a standard deviation of 5.1 microns; the petals are white; the fruiting heads, which have diameters ranging from 3.75-4.24 mm, consist of fruits that usually have on their dorso-apical surfaces a single sulcus.

*Type locality*.—Eastern United States. Without definite locality. Schultes and Schult.

*Distribution*.—This taxon is found from coast to coast, and from the middle latitudes of the United States northward into Canada (fig. 4). Its distribution in North America is similar to that of *A. plantago-aquatica* L. var. *michaletii*, except that the variety *americanum* is found to the south in states in which the variety *michaletii* has not been reported: Arizona, Kansas, Missouri, Iowa, Michigan, and Pennsylvania. Its limits in the southeast are well-defined. Here it is clearly replaced by *A. plantago-aquatica* L. var. *parviflorum*, which is ubiquitous in the southeastern states.

This variety is not found in Europe, but is common in China, Japan, Manchuria, Mongolia, and Siberia (fig. 3). It has also been found in Afghanistan, Kashmir, and India.

*Discussion*.—Since the early eighteen-hundreds American collectors have been describing populations of American *Alisma* plants that are different from *A. plantago-aquatica* plants of Europe. The American plants were separated from their European counterparts by having such characteristics as oval-cordate leaves with nine nerves, white petals, or short petioles and peduncles, with white nerved foliage.

The leaf characteristics are present in the *Alisma* populations of both continents. The corolla color seems to be a valid character inasmuch as the European plants are generally described as having a pink or purplish corolla in contrast to the white corolla in this new American taxon.

In general the American authors have tended to give this new American population the rank of species. However, in his monograph on *Alisma*, Samuelsson stated that he did not consider this American entity to be of

species rank, and he reduced it to a sub-species. He separated this new sub-species from *A. plantago-aquatica* on the basis of its somewhat smaller anthers and pistils.

The results of this investigation tend to supplement Samuelsson's work on this taxon except that it has been reduced to varietal rank and the proper varietal name has been assigned to it. To Samuelsson's diagnostic characteristics for the taxon this revision adds the relatively small size of the fruiting heads and the small size of the sepal guard cells. Despite this increase in the number of distinguishing characteristics, this taxon has been only considered as a variety because of the minuteness of the variations in contrast to the over-all uniformity of the plants' morphological features.

Samuelsson also described a new sub-species from eastern Asia, *A. plantago-aquatica* ssp. *orientale*, with blossoms smaller than those of the European *A. plantago-aquatica*. The plants from Asia examined in this study indicate that these Asiatic plants are also members of the variety *americanum*.

It seems likely that this variety is derived from *A. plantago-aquatica* var. *michaletii*. Chromosome counts and the lengths of sepal guard cells determined in this investigation indicate that the plants of this variety are diploids ( $2n = 14$ ). However, a few plants with essentially the same diagnostic characters, have been determined to be tetraploids (Heiser & Whitaker, 1948; Brown, 1946). This scattered occurrence of tetraploids in the parental diploid population may be indicative of the considerable age of the *Alisma* genus. Other indications of the relatively old age of the genus may be the wide dispersal of the *Alisma* populations over the earth, the polytypic, but continuous, nature of these populations, and their partially polyploid condition (Cain, 1944).

*Specimens examined* (total: 570).—United States. COLORADO: Piedra, C. F. Baker n. 138 (type) (GH, US). ARIZONA: Flagstaff, J. N. Adams 1910 (WIS). CALIFORNIA: Two miles north of Davis, Yolo Co., roadside ditch near rice field, W. Russell 8/16/48 (IND); north of Davis, Yolo Co., in a rice field (IND); C. B. Heiser Jr. n. 1965 (IND, UC); Six miles northwest of Chico, A. A. Heller 7/31/14 (F, NEB). IDAHO: Vicinity of Hope, A. A. Heller 8/16/92 (F). UTAH: Ogden, Wm. Cleburne 8/15/73 (NEB). IOWA: Marquette, W. L. Tolstead 8/31/33 (NEB); Johnson Co., T. J. & M. F. L. Fitzpatrick 8/4/95 (F). NEBRASKA: Kennedy, Cherry Co., Rev. J. M. Bates 1894 (NEB); Halsey, Thomas Co., R. J. Pool & Cyrus Williams June, 1911 (NEB). MISSOURI: St. Francis river, S. E. Stull n. 735 (F); six to seven miles southeast of Vienna, J. A. Steyermark 6/30/39 (F). ARKANSAS: Magnet Cove, Hot Spring Co., Delzie Demaree n. 17866 (F). KENTUCKY: Poor Fork Post Office, Harlan Co., T. H. Kearney n. 134 (F). ILLINOIS: One-half mile east of Mt. Carmel, R. M. Tryon Jr. n. 2818 (F). SOUTH DAKOTA: Twelve miles north of Camp Crook, S. S. Viher n. 33 (F). MINNESOTA: Near Duluth, Olga Lukela n. 1624 (F). WISCONSIN: Maribel, H. C. Benke n. 3848 (F). MICHIGAN: North of Cork Lake, F. C. Gates n. 15420 (F). INDIANA: Dune Creek, D. C. Peattie n. 2080 (F); Lake Co., H. H. Smith n. 5725 (F). PENNSYLVANIA: Island opposite north Harrisburg, J. K. Small 7/9/88 (F). NEW YORK: Binghamton, G. F. Millspaugh (F). MASSACHUSETTS: Bedford, H. K. Svenson & A. N. Steward 8/15/29 (F). MAINE: Estuary of Cathance River, Sagadahoc Co., N. C. Fassett n. 13 (F).

Asia. JAPAN: Sapporo. Y. Takewobn, August, 1883; S. Arimoto 7/5/03 (MO). CHINA: South of Yunnan-fu, between Hsiao-Magai and Hsiao-sing in the Yunnan Province, Hendel-Mazzetti n. 5691 (US); border of Yunnan-fu, E. E. Maire n. 1139; Mengtze, A. Henry n. 9967. MONGOLIA: Dojan. J. Eriksson n. 229 (US). MANCHURIA: Hanke-See, Turga Roche, H. Bohnhof n. 233 (NY).

## ALISMA GRAMINEUM Gmelin

Figs. 1, 8

*A. gramineum* Gmelin ex Flora Badensis Alsatica 4:256. 1826.

Perennial; from a corm 1.4 cm or rarely more in diameter, the lateral and basal surfaces covered with coarse fibrous roots; leaves 3-50 cm long, 2-20 mm wide, arising from the upper surface of the corm, enveloping the inner petiole and scape bases; petiole sheaths 5-15 mm wide at base, but tapering abruptly to 1-3 mm over most of their length; lamina linear-lanceolate to narrow-lanceolate, 1-25 cm long, 2-20 mm wide, expanding from the distal ends of the petiole; scapes 3-50 cm high, emerging from the central area of the upper surface of the corm, developing 3-5 scarious-bracted verticils, each with 3-5 main branches; panicle lax and open, often partially decumbent, rarely exceeding 35 cm in diameter, scantily branched, the foreshortened branches appearing to terminate abruptly in bracteate umbels of pedicels; thickened pedicels 1.3 cm long, reflexed or strict; flowers with 3 herbaceous sepals sub-equalling the 3 evanescent rose or purple petals; stamens 6; achenes 5-20 in a ring on a flattened receptacle, each with two sulci less than 0.1 mm deep on the dorso-apical surface; fruiting heads 3.4 mm in diameter.

*Type locality*.—Alsace-Baden region. "Dachsland." [T.: Icon. Loes. Fl. Pruss. tab. 62, p. 193. (bona.)]

*Distribution*.—Individuals of this species are found in sub-boreal habitats throughout the world. The center of the distribution seems to be in Quebec, but it has also been widely collected in Scandinavia (fig. 1). A few representatives have been collected in Siberia, Japan, and China at the extremities of the distribution. It is widely found in Ontario, Saskatchewan, Minnesota, Wisconsin, New York, North Dakota, and South Dakota (fig. 8). In Europe it is also found in Germany, France, Denmark, Estonia, Finland, and Austria.

*Discussion*.—The hypothetical origin of this species is in North America, where it is common at sub-boreal latitudes. From North America it may have migrated to northern Europe, through Scandinavia, where it is widespread.

In North America *A. gramineum* apparently hybridizes with *A. plantago-aquatica*, although it is separated from the latter species by its concurrent undulate scapes, three ridged fruits, purplish corolla, narrow leaf-blades, and its relatively wide umbels. Serology tests indicate specific differences between this taxon and *A. plantago-aquatica* L.

Principally on the basis of size, two varieties of the species in North America have been described. The larger of these varieties, *angustissimum*, is limited to North America. It has leaves with relatively wide petioles and lamina. The leaves of the variety *graminifolia* have lamina and petioles that are commonly one-half or two-thirds the width of the leaves in *angustissimum*. Cytological studies by the author and others (Erlandson, 1946; Tschermak-Woess, 1948—see Baldwin & Speese, 1955) indicate that the plants of this species are diploid ( $2n = 14$ ). All of the sepal guard cells measured in this group were found to be similar in size to those of the diploid plants in *A. plantago-aquatica* L.

It was observed in both varieties that petioleless plants were often collected in the same areas on the same dates that the more common petioled plants were collected. Collections in the same areas of the petioled *angustissimum* plants and the petioleless or gramineous-leaved plants revealed

that the widths of the blades in both kinds of plants were very similar. Moreover, occasional gramineous plants had a few leaves that widened at their distal ends into small blades. In some of these collections notes were made indicating that the gramineous plants grew in deeper water than the petioled plants. This same relationship between petioled and non-petioled plants also held true for the variety *graminifolia*. The conjecture was made that the gramineous plants are water modifications of the petioled plants, although more data are needed on this point.

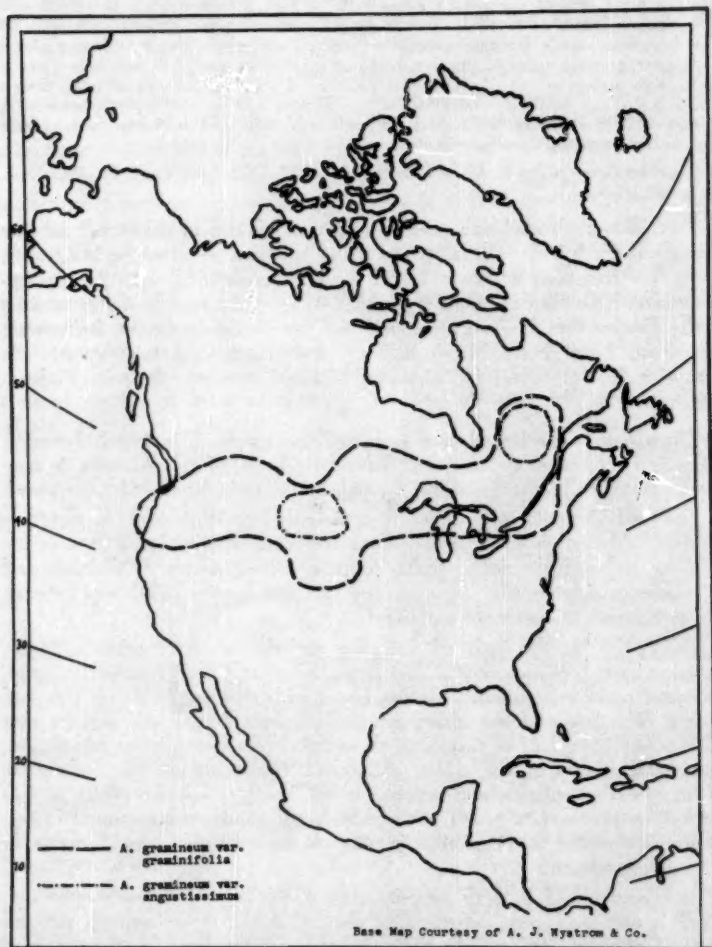


Fig. 8.—Boundaries of the North American distribution of *Alisma gramineum* Gmelin.



## KEY TO THE VARIETIES OF ALISMA GRAMINEUM

- A. Leaf petioles, when present, are 1-3 mm wide. Lamina are 1-5 mm broad. Pedicels are usually erect and umbels are rather compact.....*A. gramineum* var. *graminifolia*  
 AA. Leaf petioles, when present, are 4-6 mm wide. Lamina are narrow-lanceolate and are 4-10 mm broad, or more.....*A. gramineum* var. *angustissimum*

*Alisma gramineum* Gmel. var. *graminifolia* (Wahlenberg) comb. nov.  
 Fig. 9

- A. plantago graminifolia* Wahlenberg ex Flora Ups. liensis 122. 1820.  
*A. Geyerii* Torr. ex Nicollet, Rep. Hydrog. Mississip.:162. 1843.  
*A. longifolium* Presl. ex Sommer Konigr. Bohman XV:XLVI. 1847. Non vidi, sed sec. Celakovsky ex Osterreich. Bot. Zeitschr. 35:415. 1885.  
*A. arcuatum* Michalet ex Bull. Soc. Bot. France 1:312. 1854.  
*A. plantago (aquatica)* L. var. *arcuatum* (Mich.) Buch. 1871 ex Abh. Nat. Ver. Bremen II:34. 1871.  
*A. plantago (aquatica)* L. var. *arcuatum* (Mich.) Buch. 1871, forma *lanceolatum* Buch. 1871 ex Abh. Nat. Ver. Bremen II:34. 1871.  
*A. plantago decumbens* Boissier ex Flora Orientalis V:9. 1881.  
*A. plantago* var. *parviflorum* (Pursh) Torr. 1824. f. *stenophyllum* Lunell 1907 ex Bot. Gaz. 43:210. 1907.  
*A. annuum* Lojac. Fl. Sic. 3:182. 1909.  
*A. coreanum* Leveille ex Fedde, Repert. Nov. Sp. 8:286. 1910.  
*A. gramineum* Gmel. ssp. *Wahlenbergii* Holmberg ex Botaniska Notiser: 207. 1921-22.  
*A. gramineum* Gmel. var. *Geyerii* (Torrey) Sam. ex Arkiv. Bot. 24A, no. 7:43. 1932.  
*A. gramineum* Gmel. var. *Wahlenbergii* (Holmberg) Raymond & Kucyniak ex Rhodora 50:179. 1946.  
*A. lanceolatum* Gray ex Gray Card Index Syst., Univ. of Minn. 1951.

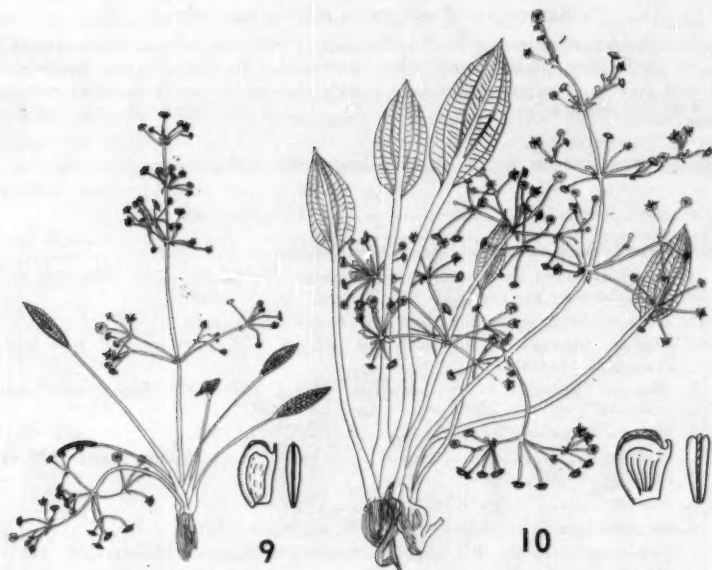
The radical leaves have petioles, ranging from 1-3 mm in width, that terminate in linear-lanceolate to narrow-lanceolate lamina that are one-third to one-half the lengths of the petioles and are commonly 1-5 mm wide; the umbels of the scape are usually dense with the angles between opposite, peripheral pedicels ranging from 150-179°.

*Type locality*.—Middle Sweden. (T.: Icon. Loes. Fl. Pruss., tab. 62, p. 198.)

*Distribution*.—Plants of this variety are common in all of the Canadian provinces and in all of the United States bordering Canada (fig. 8). Also, in the United States it has been found as far south as Nebraska, Wyoming, and South Dakota. In Europe it is widely distributed in Denmark, Sweden, Finland, and in the Baltic provinces of Russia (fig. 1). Individuals of the variety have also been collected in Germany, France, and Austria.

*Discussion*.—This variety is characterized by its relatively small radical leaves and its reduced, often partially decumbent inflorescence. The radical leaves of the emergent plants are petioled, whereas the immersed plants have gramineous leaves with blade-widths nearly the same as those of the petioled plants.

Apparently the plants of this variety are more heterogeneous than those in *angustissimum* as they migrated from North America to Europe.



Figs. 9, 10.—9. *Alisma gramineum* Gmelin var. *graminifolia* (Wahlenberg) comb. nov. Habit, x 1/5; achenes, x 4. 10. *Alisma gramineum* Gmelin var. *angustissimum* (D. C.) comb. nov. Land Form. Habit, x 1/5; achenes, x 4.

*Specimens examined* (total: 294).—Canada. QUEBEC: Boucherville, comté de Chambly, Marie-Victorin & Rolland Germain n. 49332 (F); on the St. Lawrence River, Marie-Victorin n. 8161, 20413 (GH); Longueuil Marie-Victorin n. 16025 (GH, CAN, US); Ile Plate near Longueuil, Marie-Victorin n. 18458 & 20402 (GH). SASKATCHEWAN: "Collected along the line of Grand Trunk Pacific Railway," John Macoun & Wm. Herriot n.76, 884 (F). ALBERTA: Kill Squaw east of Ribstone Creek, J. Macoun & W. Herriot n. 76883 (CAN, F).

United States. NEW YORK: Chaumont Bay, Jefferson Co., W. C. Muenscher & B. Maguire n. 1841 (F); Jefferson Co., Lake Ontario near Chaumont, Fernald, Wiegand, & A. J. Eames n. 14122 (GH). MINNESOTA: Wabasha Co., near Teepeota Point, N. C. Fassett & N. Hotchkiss n. 2719 (WIS). SOUTH DAKOTA: Roberts Co., east of Wilmot, W. H. Over n. 15412, and Meade Co., n. 17430 (US). NORTH DAKOTA: York, Benson Co., J. Lunell 7/5/06 (F); Leeds, Benson Co., J. Lunell 7/27/06 (F, GH, US); north of Falkirk, F. P. Metcalf n. 450 (US). NEBRASKA: "Frenchman Creek to Rocky Mountains," E. Cowe, 1874 (GH). MONTANA: Glasgow, J. W. Blankinship 7/17/00 (GH). UTAH: Salt Lake City, Marcus E. Jones 7/16/80 (F); Salt Lake Co., Ft. Douglas, Mrs. M. S. Clemens 1909 (GH, NY). NEVADA: Elko & Battle Mountain, A. E. Hitchcock n. 948 & 624 (US). OREGON: Near Dalles City, W. N. Suksdorf n. 635 (GH, US). WASHINGTON: Klickitat Co., W. N. Suksdorf n. 4039 (F).

Europe. SWEDEN: Lake Mälaren, Sandvik, G. Björkman 8/19/17 (US, NY, UC); Södermanland, Carl Blom 6/8/16 (MO). ESTONIA: Mouth of Parnu River, Edm. Spohr 10/8/36 (US). GERMANY: West Germany, H. V. Leonhard date 1855 (MO). FRANCE: Étang de Trou-Sale, E. Jeanpert 2/18/90 (F); Étang de St. Quentin, E. Jeanpert 10/9/99 (F); Rhone, M. Gandoger, August 1876 (MO). CZECHOSLOVAKIA: Southwest Bohemia, Celakovsky (MO).

*Alisma gramineum* Gmelin var. *angustissimum* (DC.) comb. nov.

Figs. 10, 11

- A. plantago* L. var. *angustissimum* D. C. ex Flor. Franc. ed. 3, III:189. 1815.  
*A. graminifolium* Ehrhardt. ex Ledebour's Fl. Ross. iv:40. 1821. (nomen nudum).  
*A. Loeselii* Gorski ex Karl Eichwald's Naturhistorische Skizze . . . 1:127. 1830.  
*A. plantago* (*aquatica*) L. var. *pumilum* Nolte ex Sched.; Sonder, Flor. Hanb. 210. 1851.  
*A. plantago* L. var. *aestuosum* Bolle ex Verhandl. Bot. Prov. Brandenburg II-IV:164. 1862.  
*A. arcuatum pumilum* Prah! ex Kritische Flora 2:204. 1890.  
*A. validum* Greene ex Pittonia IV:158. 1896. (type specimen).  
*A. plantago* (*aquatica*) L. var. *arcuatum* (Mich.) Buch. 1871, f. *angustissimum* Aschers & Graebn. ex Synops. Mitteleur. Flora 1:382. 1898.  
*A. arcuatum* Lunell ex Bot. Gaz. XLIII:210. 1907.  
*A. arcuatum* Michalet var. *angustissimum* (Aschers. & Graebn.) Lunell ex Bot. Gaz. 43:211. 1907.  
*A. arcuatum* Michalet var. *lanceolatum* (Buch.) Lunell ex Bot. Gaz. 43:211. 1907.  
*A. Geyerii angustissimum* (A. & G.) Lunell ex Bull. Leeds Herb 2:5. 1908.  
*A. Geyerii lanceolatum* (Buch.) Lunell ex Bull. Leeds Herb 2:5. 1908.  
*A. arcuatum pumilum* (Prah!) Lunell ex Amer. Midl. Nat. 4:163. 1915.  
*A. Geyerii* var. *giganteum* Lunell ex Amer. Midl. Nat. 4:163. 1915.  
*A. submersum* Adamow ex Mem. Inst. Agronom. Bellarussie III:450-456. 1924.  
*A. Geyerii pumilum* Lunell 1908 ex Gray Card Index, Univ. of Minn. 1951.

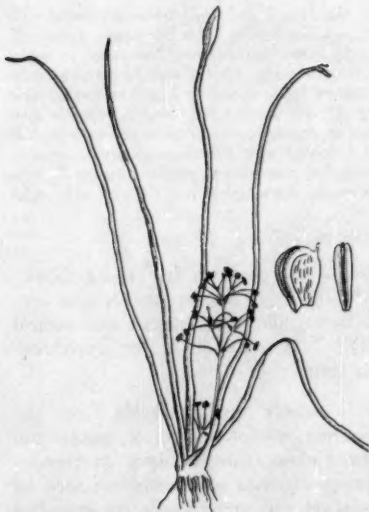


Fig. 11.—*Alisma gramineum* Gmelin var. *angustissimum* (D. C.) comb. nov. Water Form. Habit,  $\times 1/5$ ; achenes,  $\times 4$ .

The radical leaves have petioles, ranging from 4-6 mm in width, that terminate in linear-lanceolate to narrow lanceolate lamina that are one-third to one-half the lengths of the petioles and are commonly 4-10 mm wide; the umbels of the scape are usually open and lax in appearance with the angles between opposite, peripheral pedicels ranging from 180-209°.

*Type locality*.—Near Gernersheim, collected by W. D. J. Koch.

*Distribution*.—With a few exceptions, found only in North America. The distribution is essentially from North Dakota to Quebec (fig. 8), with a few individuals being found in California, Nevada, Oregon, Alberta, Saskatchewan, Montana, Wyoming, and South Dakota.

*Discussion*.—This variety is separated from var. *graminifolia* by its

larger size and its limited geographical distribution. The leaves and inflorescence of plants in this variety are larger than those in var. *graminifolia* and the plants occur mainly in a relatively confined area from North Dakota to Quebec province. The emergent plants are petioled, whereas the immersed plants are gramineous.

*Specimens examined* (total: 50).—Canada. QUEBEC: Longueuil, Co. De Chambly, eaux argileuses autour de l'île Plate, Marie-Victorin & Rolland Germain n. 33934 (F); Île Plate, near Longueuil, 1918, Marie-Victorin n. 8162 (GH, US). SASKATCHEWAN: Moose Jaw, 1895, J. Macoun n. 14001 (CAN); Ribstone Creek, J. Macoun & W. Herriot n. 76884 (CAN).

United States. NORTH DAKOTA: Leeds, J. Lunell 8/8/07 (F); Benson Co., Leeds, Lunell n. 39, 7/18/06 (GH, US, RM). SOUTH DAKOTA: Spink Co., Cottonwood Lake, South Bass Pond, W. H. Over n. 17182 (US); "In the Sioux River," Brookings, J. J. Thornber 6/30/94 (NEB). MONTANA: Great Falls, R. S. Williams n. 1080 (US). WYOMING: C. L. Porter & B. F. Miller n. 6041 (RM).

#### ALISMA LANCEOLATUM Withering

##### Fig. 12

*A. lanceolatum* Withering ex Bot. Arrang. Brit. Plants. Ed. 3.II:362. 1796.

*A. verticillatum* Dulac ex Flore du département des Hautes-Pyrenees. . . . Plantes vasculaires spontanees, etc. 1:45. 1876.

*A. ceretanica* Sennen. Bull. Soc. Bot. France 1916, lxiii:134. (1917).

*A. plantago* ssp. *stenophyllum* Holmberg ex Skandnaviens Flora. H.1:109. 1922.

*A. stenophyllum* Samuelsson ex Svensk. Bot. Tidskr. XVI:39. 1922.

*A. rariflorum* Samuelsson ex Arkiv för Botanik. Band 24A, N:0 7:32-33. 1932.

Perennial, from a corm 1.4 cm in diameter, the lateral and basal surfaces covered with coarse fibrous roots; leaves 5-20 cm long, 1.5 cm wide, arising from the upper surface of the corm, enveloping the inner petiole and scape bases; lamina ovate-lanceolate to ovate, with apices acute and bases cuneate-attenuate, 1-10 cm long, 1.5 cm wide, expanding from the distal ends of the petiole; scapes 1-7 decimeters high, emerging from the central area of the upper surface of the corm, developing 3-7 scarious-bracted verticils; panicle sub-spherical, up to 4 dm in diameter with branches appearing to terminate in bracteate umbels of pedicels; slender pedicels, 1-2 cm long, strict; flowers with 3 herbaceous sepals approximately one-half the length of the apically triangular, rose-colored petals; stamens 6; with one or rarely two sulci less than 0.1 mm deep on the dorso-apical surface, and with styles fixed near the middle of the ventral surface.

*Type locality*.—British Isles. (T.: Icon., Gerard, 337.2).

*Distribution*.—Individuals of this species are common in France, Spain, Corsica, Italy, Yugoslavia, and England (fig. 1). The species is also represented in North Africa (fig. 1) and throughout southeastern and central Asia, as well as in Asia Minor (fig. 2). The species has been introduced into North and South America in recent times.

*Discussion*.—This European species is mainly distinguishable from the other European taxa, *A. plantago-aquatica* var. *michaletii* and *A. gramineum* var. *graminifolia*, by its leaves, which have either narrow-elliptic or narrow-spatulate lamina. The leaves of *A. plantago-aquatica* var. *michaletii* tend to be ovate-cordate, while those of *A. gramineum* var. *graminifolia* are strap-like and taper abruptly at both ends.

In addition to this leaf character, this species has been described as being a tetraploid (Erlandsson, 1946), while *A. plantago-aquatica* var. *michaletii*

and *A. gramineum* var. *graminifolia* are diploids. Erlandsson suggested that this polyploid species may have evolved from its more widespread neighboring taxon, *A. plantago-aquatica* (var. *michaletii*).

Actually, if this taxon is related to the variety *michaletii* in the same manner that the variety *americanum* is, then it seems probable that *A. lanceolatum* is merely a diploid with occasional polyploids occurring in the periphery of the distribution of the diploid taxon. The distribution of this species includes the Mediterranean countries of Europe and Africa, and the Balkan countries. Its boundaries are to the south of those of *A. gramineum* var. *graminifolia* but it lies within the distribution of *A. plantago-aquatica* var. *michaletii*.

*Specimens examined* (total: 33).—EUROPE. ENGLAND: Kew, J. T. Tilleggrideger, 1880; A. Bennett, Aug. 1881; Mrs. Annie Nethercott 1872 (F). CORSICA: "La Corse," H. Bruyas, June 1882 (NEB); Paul Aellen 7/27/33 (MO). FRANCE: "Les Domes, Le Plantay," M. Gandoger, Aug. 13, 1871; Ramboillet, Jeanpert Aug. 18, 1894 and July 12, 1908, environs of Paris (F). GERMANY: Magdeburg, H. Eggert 7/4/67 (MO); Runth-Weimar, July, 1902; Blasewartz, July 5, 1862. BELGIUM: Dervildeman, July, 1926. AUSTRIA: Dörfler n. 3916; lower Austria, F. A. Tscherning, July, 1899 (F); HUNGARY: "Toky," J. Gustav; SWEDEN: Carl Sandberg, August, 1929. RUSSIA: E.



Figs. 12, 13.—12. *Alisma lanceolatum* Withering Habit,  $\times 1/5$ ; achenes,  $\times 4$ . 13. *Alisma canaliculatum* A. Br. & Bouche Habit,  $\times 1/5$ ; achenes,  $\times 4$ .



Matveeva, June 20, 1931. SPAIN: A. Cabellero, July 4, 1932 (MO). MADEIRA: Sao Jorge, Trelease, June 17th & 18th, 1896 (MO). AZORES: Trelease 959a (MO). CRETE: Lassithi, M. Gandoger year 1914 (MO); La Canes, M. Gandoger year 1914 (MO).

ALISMA CANALICULATUM A. Br. & Bouche

Fig. 13

*A. canaliculatum* A. Br. & Bouche ex A. Braun in Index Sem. Hort. Bot. Berolin.:2. 1862.

*A. plantago* L. var. *canaliculatum* A. Braun in Index Sem. Hort. Bot. Berolin. (Appendix 4) 1867.

Perennial; from a relatively small corm 5-10 mm or rarely more in diameter, the lateral and basal surfaces covered with coarse fibrous roots; leaves 5-25 cm long, 1-5 cm wide, arising from the upper surface of the corm, enveloping the inner petiole and scape bases; petiole sheaths often 5 mm or more wide at base, but tapering abruptly to 2-3 mm over most of their length; lamina noticeably narrow-spatulate, 2-15 cm long, 1-5 cm wide, expanding from the distal ends of the petiole; scapes 2-6 dm high, emerging from the central area of the upper surface of the corm, developing 6-8 scarious-bracted verticils, each with commonly 3 main branches; panicle rather narrow, rarely exceeding 15 cm in diameter, with the branches appearing to terminate in bracteate umbels of pedicels; pedicels 5-20 mm long, strict; flowers with 3 herbaceous sepals sub-equaling the 3 evanescent white petals; stamens 6; achenes 5-20 in a ring on a flattened receptacle, each with one sulcus, 0.2 mm or more deep, on the dorso-apical surface, and with styles fixed at the ventral-apical surface; fruiting heads 3-5 mm in diameter.

*Type locality*.—Near Yokohama, Japan. (T.: A. Braun 1862, B.). This type destroyed in World War II.

*Distribution*.—The distribution is concentrated in Japan and in its coastal island groups (fig. 3), but the species is also found in the Liu Kiu Isles, China, Manchuria, Siberia, India, and Kashmir.

*Discussion*.—This species is unique in the shape of the plants' oblanceolate leaf-blades that are long-attenuated at the proximal end. In addition to this these plants have fruits with a dorso-apical sulcus that is visibly deeper than that in any other *Alisma* taxon. In Japan, the Ryukyu Islands, and in China this species is associated with the more widespread *A. plantago-aquatica* var. *americanum*.

Viable fruits from only one collection of this taxon were available for this study. Mitotic figures from the seedlings indicate tetraploidy ( $2n = 28$ ). The average length of the guard cells in several of the herbarium specimens of this entity has been found to be 57 microns. This represents an eighteen to a fifty percent increase over the guard cell lengths found in the varieties of *A. plantago-aquatica*. Further investigation will have to be made to determine whether or not the majority of plants in the taxon are tetraploids.

*Specimens examined* (total: 33).—Asia. JAPAN: Nagasaki, Herb. Petropolit. Maximowicz, 1863 (NY); Tokyo, J. Matsumura 6/7/78; K. Shiota n. 6813, n. 9837, n. 9137; Sapporo, S. Arimoto 9/5/03 (MO). RYUKYU ISLANDS: "Kushi-mura, along Henoko River," E. H. Walker, S. Tawada, and T. Amano (US); W. D. Field & O. G. Loew n. 94 h; Schlammboden n. 81. CHINA: Kiangseu Province, Nanking, E. D. Merrill (R. C. Ching collection 3927) (UC); Y. R. Keng n. 1035 & n. 546; W. Hupeh, E. H. Wilson n. 2579 (NY). MANCHURIA: B. V. Skvorizov; Lac Hanka, Hugo Bohnhoff n. 300 (NY). INDIA: W. Koelz n. 9012 & n. 7499; R. R. Stewart 1839. SIBERIA: M. Bohnhoff.

## REFERENCES

- ARNOLD, C. A. 1947—An introduction to paleobotany. pp. 333-34. McGraw-Hill Book Company, Inc. New York.
- ASCHERSON, P. AND P. GRAEBNER 1897—Synops., Mitteleur, Flora I:382.
- AXELROD, DANIEL I. 1952—A theory of angiosperm evolution. *Evolution* 6:29-59.
- BALDWIN, J. T. AND BERNICE M. SPEESE 1955—Chromosomes of taxa of the Alismaceae in the range of Gray's Manual. *Amer. J. Bot.* 42:406-410.
- BROWN, W. V. 1946—Cytological studies in the Alismaceae. *Bot. Gaz.* 108:262-267.
- BUCHENAU, FRANZ 1903—Alismaceae. Engler's *Die Pflanzenreich* 16(IV.15):1-66.
- CAIN, STANLEY A. 1944—Foundations of plant geography pp. 12-15, 185-192, 415-417, 430-437. Harper & Brothers, New York & London.
- CHESTER, K. STARR 1937—A critique of plant serology. *Quart. Rev. Biol.* 12:19-46, 165-190, 294-321.
- ERLANDSSON, STELLAN 1946—Chromosome studies of three *Alisma* species. *Svensk Botanisk Tidskrift*. Bd. 40, H.4. pp. 427-435.
- FERNALD, M. L. 1946—The North American representatives of *Alisma plantago-aquatica*. *Rhodora* 48:86-96.
- 1950—Gray's manual of botany. 8th ed. pp. 83-84. American Book Company, New York.
- HEISER, C. B., JR., AND T. W. WHITAKER 1948—Chromosome number, polyploidy, and growth habit in California weeds. *Amer. J. Bot.* 35:179-186.
- LANJOUW, J. AND A. STAFLEU 1954—Part I. The Herbaria of the World. *Index Herbariorum*. 2nd. ed. Chromica Botanica Co., Waltham, Mass.
- LUNELL, J. 1907—The Genus *Alisma* in North Dakota. *Bot. Gaz.* 43:209-213.
- 1908—New matter of the season. *Bull. Leeds Herb.* 2:5-8.
- 1915—The vascular plants of North Dakota. *Amer. Midl. Nat.* 4:152-165.
- MICHEL, MARCO 1881—Alismaceae. *D. C. Monog. Phan.* 3:29-38.
- OLESON, E. M. 1941—Chromosomes of some Alismaceae. *Bot. Gaz.* 103:198-202.
- PICHON, M. 1946—Sur les Alismatacées et les Butomacées. *Not. Syst. (Paris)* 12:170-183.
- RAFINESQUE-SCHMALTZ, CONSTANTINE 1808—*Med. Repos.* New York 2:5.
- SAMUELSSON, GUNNAR 1932—Die Arten der Gattung *Alisma* L. *Ark. Bot.* 24A. N:0-7, 24:1-46.
- 1933—*Alisma* L. *Die Pflanzenareale*, 3. Reihe, H.8. pp. 88-90. Jena.

## The Genus *Malacothrix* (Compositae)

Elizabeth W. Williams

University of Southern California, Los Angeles

*Malacothrix* is a genus of Compositae belonging to the Chicory tribe. It is native to western North America, where it occurs rather widely distributed in nine western states and parts of Mexico. It is not commonly cultivated, although Bailey (1941), states that it is sometimes grown for ornament and lists three species. The most conspicuous member of the genus, and also the most commonly occurring, is *M. californica*, popularly called the Desert Dandelion. It presents a rather handsome appearance, having conspicuous light yellow heads and a basal rosette of narrowly divided leaves. As here outlined the genus is divided into 11 species and 15 varieties.

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### HISTORICAL BACKGROUND

The genus was established by de Candolle in 1838. De Candolle's description was based on a dried specimen, originally collected in California by Douglas, and sent to him by the Horticultural Society of London. The generic name is from the Greek words meaning soft and hair. In 1841 Nuttall described *Leptoseria sonchoides*, *Malacomeris incanus*, *Leucoseris saxatilis*, and *Leucoseris tenuifolia*. These species were later transferred to *Malacothrix*, and the genera listed as synonymous, by Torrey and Gray (1843).

Other species were described as other collections were made by individuals, as Fendler in New Mexico, Coulter in California, or as a result of expeditions such as the Geological Exploration of the Fortieth Parallel (Eaton, 1841), Exploration and Survey of the Valley of the Great Salt Lake of Utah (Torrey, 1852), and the Pacific Railroad Reports (Gray, 1860).

Of the 28 specific names that have been published, 14 were published by Asa Gray. In 1874 Gray, having more material to work with, revised the genus and listed 11 species. This time he divided it into two groups, *Malacolepis* and *Eumalacothrix*, according to the nature of the involucre. Of these species, two have been excluded (both by Gray himself), one reduced to synonymy, and one reduced in rank. In the present paper one other species (*M. torreyi*) has been reduced to varietal rank.

Notable among collections made during the latter part of the nineteenth century and early twentieth century were those of Marcus E. Jones and Edward L. Greene. Jones collected a large number of plants ranging from Baja California, north through California, New Mexico, Arizona, Nevada, Utah, and Idaho. Greene collected fewer plants, but of these he described four species as new (1885), three of which are from islands off the coast of California. However, in the present study, they are either reduced to varietal rank or to synonymy.

Since 1900 a few additional species and varieties have been described, and a great many more collections have been made. The most complete, comparatively recent, treatment of the genus is by Hall (1907).

#### GEOGRAPHICAL DISTRIBUTION

The genus has generally been considered as being restricted to western North America. However, *M. coulteri* has evidently been introduced into Argentina and Chile, for it was collected by Walter Fischer, No. 144 (US), in the Rio Negro Valley, Argentina, in 1914. In 1926 it was collected by F. Claude Joseph in Chile, No. 4503 (US 1444369) and again in Chile in 1938 by C. R. Worth and J. L. Morrison (UC 629830).

*Malacothrix* is well represented in California. There are only two species that are not found in the state. These are *M. fendleri*, which occurs in Arizona and New Mexico, and *M. xanti*, occurring in Baja California. *M. californica*, including var. *californica* and var. *glabrata*, is the most widespread and commonly occurring species. *M. foliosa*, *M. blairii*, and *M. saxatilis* var. *implicata* are found only on the islands off the California coast.

The range of the genus in North America is from Lower California and Sonora north through California into southern Oregon and Idaho, east to Utah, Colorado, New Mexico, and into western Texas (figs. 1-9). The range of habitats is from seashore and desert to montane. Ecological associations are quite varied. The distribution of the species and varieties is given in detail in the *Taxonomic Treatment*.

A sufficient number of herbarium sheets from various herbaria has been examined and the data recorded to give a comprehensive picture of the geographical distribution of the genus. Maps of the range of each of the species have been plotted on the basis of the specimens studied.

Herbarium specimens of *Malacothrix* were kindly made available for this study by the following institutions. Abbreviations of herbaria are those used in Index Herbariorum (Lanjouw and Stafleu, 1954) as indicated.

CAS—California Academy of Sciences; LA—University of California, Los Angeles; UC—University of California, Berkeley; AHFH—Hancock Herbarium, Allan Hancock Foundation, University of Southern California; GH—Gray Herbarium of Harvard University; USC\*—Botany Department Herbarium, University of Southern California; LAM—Los Angeles Museum Herbarium; DS—Dudley Herbarium, Stanford University; POM—Pomona College Herbarium; US—United States National Herbarium; RM—Rocky Mountain Herbarium.

#### DISCUSSION

*Malacothrix*, though not a large genus, exhibits numerous variations and intergrading forms. There are few morphological characters which are clear-cut and distinct. Throughout the genus, flower color is noticeably unstable. For instance, the flowers of *M. floccifera* are generally white. The ligules may, however, be white streaked with pink on the outside, or the innermost may be yellow, or occasionally the whole head is yellow. In this case ligule color is not considered sufficiently important to warrant varietal distinction. In the two normally yellow-flowered species, *M. clevelandi* and

\* Abbreviation not listed in Index Herbariorum, but not preoccupied.

*M. californica* white flowers occasionally occur. In the Mexican collections of *M. californica* var. *glabrata* the ligules are white, usually with pink streaks on the outer side of the outer ligules, as compared with the consistently yellow ligules of the more northern plants of the species, although pink streaks on the outer ligules occur occasionally in var. *californica*. In *M. blairii* the ligules are rose-pink.

Most species are herbaceous. *M. blairii*, the most distinctive member of the genus, is a perennial, woody shrub native to San Clemente Island.

The form of the leaf varies from a simple, broad, sinuate leaf in *M. blairii* to a leaf divided into narrow linear segments in *M. californica*. In some cases the leaves are succulent. Vestiture may vary from glabrous to hairy or white tomentose. In *M. floccifera* the leaves are speckled with tufts of white wool. No doubt these were the basis for the name.

The nomenclatural types for this study were obtainable except in a few cases. Where the type was not examined a notation is made to that effect. Also, a careful search of the literature has been made to locate typifications by earlier authors.

Nomenclatural changes made for the first time are: (1) *M. altissima* listed as a synonym under *M. saxatilis* var. *tenuifolia*; (2) *M. insularis* listed as a synonym under *M. foliosa* var. *foliosa*; (3) *M. squalida*, *M. indecora*, *M. succulenta*, *M. arachnoidea*, and *M. torreyi* reduced to varietal rank.

This study has largely been concerned with species that have previously been assigned to the genus. In regard to genera closely allied to *Malacothrix* an attempt was made during the preparation of this paper to show in chart form some of the outstanding morphological and distributional variations between them. This, however, was abandoned due to the large number of genera of the Cichorieae, all of which seem to be fairly closely related, and to the difficulty of obtaining data for the larger genera that would be up to date and world-wide in scope. It was found that this would have involved a more detailed study than was possible at the present time.

The Cichorieae constitute a botanical taxon which exhibit integrations of morphological characteristics. One probable explanation of this is that they represent lines of evolutionary development that are young as compared to plant taxa in general. The closely connecting links between species and genera are still extant as contrasted with genera and species which represent lines of ancient evolutionary development where many of the connecting links between closely allied groups have become extinct, leaving the existing representatives well defined in their category. Rapid dispersal of members of the Cichorieae occurs over varied ecological environments. Further complicating the picture, apomixis has been reported to occur in *Crepis*, *Hieracium* and *Taraxacum* and perhaps other genera of the tribe as well.

*Hieracium* is the largest genus of the Cichorieae. *Crepis* ranks next with 196 species described in Babcock's monograph, also a number of new species of *Crepis* have been described since this was published. Regarding the Cichorieae, Babcock (1947) states:

... within the tribe the relationships of the genera are very complex and no system exists which has successfully divided it into subtribes. As a first step toward a critical revision of this tribe, Stebbins (unpublished) has prepared a tentative reclassification of the sixty-four genera in the group, based on preliminary studies of comparative morphology, geographic distribution, and chromosome numbers, . . .



Four small genera resembling *Malacothrix* in appearance and overlapping in geographic range are: (1) *Anisocoma*, a monotypic genus resembling *M. coulteri* quite closely in general appearance, range California, Arizona, Nevada. It has plumose pappus as compared with barbellulate pappus in *Malacothrix*. (2) *Glyptopleura*, with two species, occurs in the deserts from Utah to California. It has beaked achenes and outer phyllaries which are foliaceous. In *Malacothrix* the apex of the achene is truncate or cupulate. (3) *Calycoseris*, also with two species, has a beaked achene, range California, Arizona and Mexico. (4) *Aspurgidium*, a monotypic genus, has brownish pappus and 30-45 persistent setae, with a range from California to Alaska. In *Malacothrix* the pappus is white, and mostly deciduous.

## SPECIES EXCLUDED

*Malacothrix platyphylla* Gray, Proc. Amer. Acad. 9:219. 1874. = *Atrichoseris platyphylla* Gray, Syn. Fl. 1, pt. 2, 410, 1884.

*M. crepoides* Gray ex J. G. Cooper, Pacif. R.R. Rept., 12:53, 1860 = *Crepis capillaris* (L.) Wallr. (Fide Babcock, 1947).

## MALACOTHRIX DC.

*Malacothrix* DC., Prodrum, 7:192; 1838. Type species.—*M. californica*.

*Leptoseris* Nutt., Trans. Amer. Philos. Soc., N.S. 7:438, 1841. Type species.—*M. sonchoides*.

*Leucoseris* Nutt., Ibid., p. 439. Type species.—*M. saxatilis*.

*Malacomeris* Nutt., Ibid., p. 435. Type species.—*M. incana*.

*Malacolepis* Heller, Muhlenbergia, 2:147, 1906. Type species.—*M. coulteri*. Based on Section *Malacolepis* in Gray, Syn. Fl. N. Amer., 1, Pt. 2; 1884.

Annual or perennial herbs or shrubs, mainly of western North America. Stems scapose or leafy, often hollow. Leaves basal or alternate, margins rarely entire. Heads up to 4 cm across, loosely cymose or paniced, rarely solitary, never sessile, buds usually nodding. Involucre cylindric to campanulate or turbinate; phyllaries ovate to linear-lanceolate, at first erect in bud, spreading in anthesis, and reflexed at maturity of achenes. Receptacle with bristles, hairs, or glabrous. Flowers few to numerous per head, yellow, white, or pink; ligules 5-cleft at summit, outermost commonly longer than inner, apex of throat usually puberulent. Style with short, spine-like hairs present along upper one-half or three-fourths of surface. Achenes 2-3.5 mm long, ranging in color from tan to dark brown, 10-16 ribbed, cylindrical, or 5 of the ribs more prominent, truncate or tapering toward base, apex flattened or cupulate, margin entire or denticulate; pappus consisting of 15-40 soft white setae, 2-4 times as long as the achenes, these clothed with short, antrorse directed, barbellulae. Inner setae somewhat united at base and falling away together, often leaving 1-8 outer stiffer setae persisting.

## KEY TO THE SPECIES

1. Phyllaries orbicular to ovate with broad scarious margins, very obtuse, only the innermost lanceolate, well imbricated; persistent pappus setae 1-4 ..... 1. *M. coulteri*
1. Phyllaries lanceolate to linear with narrow pale margins, sparingly imbricated.
2. Pappus setae of two kinds: Ring of deciduous inner setae, and 1-5 outer persistent setae.
3. Leaves linear-filiform, or pinnatifid into linear filiform segments; persistent pappus setae 2 ..... 2. *M. californica*
3. Leaves broader, toothed; persistent pappus setae 1-8.
4. Stems slender at apex (0.5 mm often), usually considerably branched and sparsely leafy.
5. Basal leaves broad (up to 4, or occasionally 5 cm across when mature); ligules white or pink streaked ..... 3. *M. xanti*

- 5. Basal leaves narrow; ligules usually yellow ..... 4. *M. clevelandi*
- 4. Stems almost the same diameter at base and apex, sparsely branched, or when considerably branched and somewhat tapering, also leafy.
- 6. Achenes 5-angled; persistent pappus setae 1-8, often 5; herbage commonly with glandular hairs ..... 6b. *M. sonchoides* var. *torreyi*
- 6. Achenes cylindric; persistent pappus setae 1; herbage without glandular hairs ..... 5. *M. fendleri*
- 2. Pappus setae all alike, deciduous.
- 7. Plants with conspicuous rosette of basal leaves; stem leaves much reduced in size; annuals.
- 8. Achenes with a deep apical cup and a ring of white teeth within a dark marginal rim; receptacle naked ..... 5. *M. fendleri*
- 8. Achenes with flattened apex, bordered by a pale rim of dentate to crenulate teeth; receptacle often with long white hairs.
- 9. Flowers yellow; leaves glabrous, usually doubly dentate ..... 6. *M. sonchoides*
- 9. Flowers pale, rarely yellow; leaves usually with flocks of white wool and once dentate ..... 7. *M. floccifera*
- 7. Plants without conspicuous rosette of basal leaves; stem leaves similar in size on lower portion of plant; annuals or perennials.
- 10. Ligules yellow; plants commonly 3 (sometimes 4) dm tall.
- 11. Leaves usually with white wool, if glabrous, oblanceolate, with margins essentially entire ..... 8. *M. incana*
- 11. Leaves glabrous, pinnatifid or coarsely toothed, with usually acute segments ..... 9. *M. foliosa*
- 10. Ligules white, pink streaked, or pink; plants 3-17 dm tall.
- 12. Heads narrowly cylindrical, 9-14 flowered ..... 10. *M. blairii*
- 12. Heads broadly campanulate, 50-90 flowered ..... 11. *M. saxatilis*

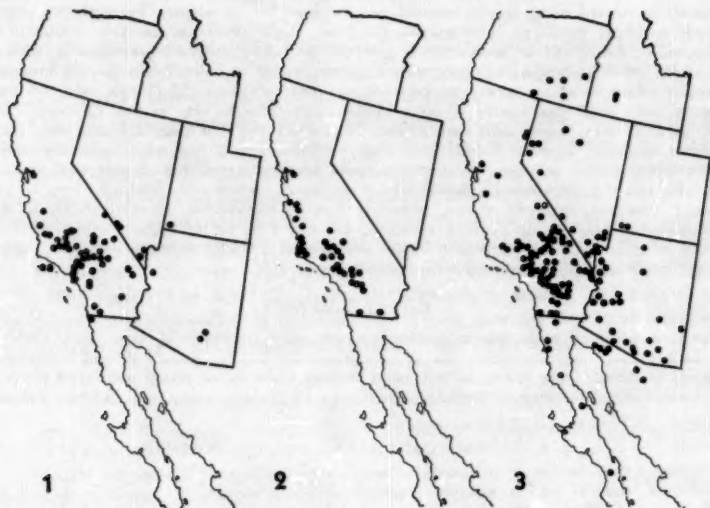
1. MALACOTHRIX COULTERI Gray, Mem. Amer. Acad., N.S. 4:113, 1849. "Snake's Head"

Fig. 1

Annual; 1-6 dm high; tap root long tapering; stem hollow, glabrous, simple, or branching at or above base, individual branches bearing single heads; leaves glabrous and glaucescent, basal and lower cauline leaves lanceolate oblong, 3-10 cm long, lobed to sinuately pinnatifid or toothed, broad or somewhat auriculate at the sessile base, often with an elongated terminal lobe; upper leaves similar in shape, but gradually decreasing in size, especially in length, with bases correspondingly more expanded and auriculate; number of heads 1-20, borne terminally on the leafy stems; a scarious ovate bract, or bracts, often present on peduncle just beneath the heads; heads subglobose, 1.5-3 cm broad; involucre 1-2 cm high, phyllaries conspicuous, silvery-scarious with linear central portion green (changing to brown), regularly imbricated in several ranks, the outer short, orbicular, the innermost oval to lanceolate with a smooth rounded apex; receptacle with slender persistent bristles; heads 70-125 flowered; ligules light yellow, or occasionally the outer ones white; corolla 1-1.5 cm long, tube 4-6 mm long, limb 1-1.5 mm wide, apex consistently 5-toothed, a few uniseriate hairs, some as long as 0.4 mm present on base of limb of corolla; style exserted 1-4 mm beyond the staminal tube; achenes brown, cylindric, 15-ribbed and 4 or 5 angled, 2-2.5 mm long, surface serrulate, apex concave, outer margin denticulate by projection of the ribs, just inside these a ring of minute colorless scarious teeth; pappus white or sordid, 5-6 mm long, 1-5 setae persistent, deciduous setae 21 to 24 in a ring.

KEY TO VARIETIES

- Cauline leaves ovate, irregularly toothed, or shallowly pinnatifid ..... a. var. *coulteri*
- Cauline leaves lanceolate, pinnately parted into remote lanceolate divisions ..... b. var. *cognata*



Figs. 1-3—Geographic distribution of *Malacothrix*. 1. *M. coulteri*; 2. *M. californica* var. *californica*; 3. *M. californica* var. *glabrata*.

#### 1 a. *M. COULTERI* Gray var. *COULTERI*

*Type*.—California, Thomas Coulter, Ex. 252 (GH, recognizable fragment, mounted on same sheet with collections by Sitgreaves, Kellogg, and Brewer—only collection cited at time of publication). *Malacolepis coulteri* (Gray) Heller, Muhl., 2:147, 1906.

Desert, dry washes, slopes and plains, California, San Joaquin Valley, and Mohave Desert, canyons of coast ranges of southern California to San Diego Co., and northern Baja California, occasional in central and western Arizona, SW. Utah and Nevada. March-May. Introduced into South America, Chile and Argentina. October-November.

#### 1 b. *M. COULTERI* Gray var. *COGNATA* Jepson, Man. Fl. Pl. Cal., 1001, 1925.

*Type*.—Santa Cruz Island, California, T. S. Brandegee 1888 (UC 92245).

Only one other specimen has been examined that had leaves characteristic of this variety. It was from Byron Springs, Contra Costa Co., California, collected by Eastwood, No. 3816 (CAS).

### 2. *MALACOTHRIX CALIFORNICA* DC., Prodrômus 7:192. 1838. "Desert Dandelion"

Annual; flowering scapes one to several from a basal rosette of leaves; tap root gradually tapering, secondary roots usually much smaller; stems terete, hollow, 7-45 cm long, green, turning light brown, or somewhat reddish, unbranched with one flowering head at apex, occasionally bearing 1-2 linear bracts 0.5-2 cm long, or sparsely to considerably branched and somewhat leafy, glabrous, or when young clothed with long soft hairs; basal leaves 2-20 cm long, sometimes entire in young plants, usually pinnately divided into as many as 12 remote filiform segments, glabrous or clothed with long soft hairs,

especially toward base; heads terminal on the branches or scapes, 1-several per plant; buds nodding; involucre campanulate, 0.5-2 cm high; phyllaries unequal, subulate to lanceolate, imbricated in several rows, glabrous or hairy; receptacle glabrous or with a few delicate short bristles, or rarely with attenuate bristles or hairs; heads 40-250 flowered; ligules yellow or white, sometimes outermost streaked red-purple, 12-25 mm long, 1-4 mm broad, tube 6-10 mm, lamina of outer ligules often twice as long as that of inner ones; styles 10-15 mm, stigma cleft only slightly (up to 0.5 mm); achenes 2-3 mm long, light brown, cylindric, tapering toward base, faintly 15-striate, 5 of the ridges sometimes more prominent, surface serrulate, apex concave, pale, bordered by a ring of pale teeth and 2, or very rarely 4, persistent pappus setae, 6-8 mm long, covered with short (0.1 mm or less long) numerous, regularly spaced, antrorsely directed barbellulae, adhering closely to the seta; inside these a ring of 7-22 subequal, 6-8 mm long setae, slightly joined at base, with irregularly spaced, somewhat longer and stouter barbellulae, many extending away from bristle at right angles, especially toward base.

## KEY TO VARIETIES

- Stems scapose; all buds arising basally; younger parts covered with long, soft, white hairs .....a. var. *californica*  
 Stems branched; buds arising in leaf axils; herbage glabrous, or young stems and phyllaries covered with tan or sordid woolly hairs .....b. var. *glabrata*

2 a. *M. CALIFORNICA* DC. var. *CALIFORNICA*

## Fig. 2

*Type*.—California, Douglas (G, isotype only seen, mounted on same sheet with 4 other collections from California. No doubt the type is in the Prodromus Herbarium of the de Candolle's in the Delessert Herbarium, Geneva).

Sandy soil, low elevations, coastal California from Contra Costa Co., S. to Santa Barbara Co., higher elevations (1000 to 5000 ft.), southern Sierra Nevada in Tulare and Kern cos., coast ranges, Ventura Co. to San Diego and Imperial cos. April-June.

2 b. *M. CALIFORNICA* DC var. *GLABRATA* Eaton, in King,  
Exp. 40th Par., 5:201, 1871.

## Fig. 3

*Type*.—Near Carson City, Nevada, 1865, C. L. Anderson (GH—on same sheet is collection from Nevada, 1865, by Serreno Watson, No. 709, of U.S. Geological Exploration of the 40th Parallel, both collections are cited in original description). *M. glabrata* (Eat.) Gray, Syn. Fl., 1, part 2, p. 422, 1884. Based on var. *glabrata* Eaton.

Frequent, sandy soil, deserts and dry washes, low elevations, Arizona, and SW. Utah, Mohave and Colorado deserts of California, San Joaquin Valley, dry eastern Sierra Nevada in California and Nevada, north into Oregon and SW. Idaho. March-June, except in Oregon and Idaho, May-July.

The character of the hairs in *M. californica* was at first thought to be different in vars. *californica* and *glabrata*. On careful examination it appears that they are essentially alike in nature, the main difference being in degree. In var. *californica* the hairs are much longer and give the appearance of being less branched. However, when the shorter hairs of var. *californica* are examined on the more central portion of the scape, it is seen that they are considerably branched, sometime almost stellate.

There seems to be a strikingly consistent difference in the color of the

hairs. Those of var. *glabrata* have a tan or tawny color, while in var. *californica* they are pure white. The two varieties can usually be separated on this character alone, although it does not hold absolutely true.

The Mexican collections of *M. californica* var. *glabrata* form a unit in themselves. The color of the ligules is the most striking difference. They are white, usually with pink streaks on the outer side of the outer ligules, as compared with the consistently yellow ligules of the more northern plants of the species, although pink streaks on the outer ligules occur occasionally in var. *californica*. Due to the nature of the branching these Mexican plants come under var. *glabrata*. All of them seem to be rather hairy; some have quite long hairs. The outer phyllaries are consistently woolly, and sometimes the leaves are even woolly. It is interesting to note that the degree of hairiness in var. *glabrata* as a whole seems to increase from north to south.

### 3. MALACOTHRIX XANTI Gray, Proc. Amer. Acad. 9:213, 1874.

Type.—Cape San Lucas, Lower California, August 1859-January 1860, J. L. Xantus 67 (GH—only collection cited).

Annual; 1.7 dm tall from a tap root somewhat thickened in mature plants; stems 1-several from base, 1.5 mm in diameter, slender, sparsely to considerably branched, glabrous, hollow; leaves in a basal rosette, 3-20 cm long, 1.4, sometimes 5 cm broad, glabrous, thin, lyrate or lanceolate, sessile or tapering below into a winged petiole, upper margin dentate, pinnately parted toward base, apex acute; cauline leaves usually few and much reduced; inflorescence loosely cymose-paniculate; heads few to several, terminal on peduncles 0.5-5 cm in length, subtended by short linear-lanceolate bracts; expanded heads 1.2 cm broad; involucre 0.5-1 cm high; outer phyllaries subulate, in 2-3 series, inner linear-lanceolate with a green center line and narrow pale margins, apex occasionally purple; receptacle umbonate, essentially glabrous; heads 30-55 flowered; ligules 8-15 mm long, 1.5-2 cm broad, tube approximately one-third length, glabrous, white, or outermost streaked with pink or purple; style 8 mm, cleft 0.8 to 0.9 mm; puberulent for almost entire length; anthers 3 mm long; achenes light brown or straw colored, 2-2.5 mm long, 0.4 mm broad, base truncate with central round pore, surface 15 striate, with 5 ribs slightly stronger, surface covered with minute antrorsely directed echinulations, apex forming a smooth walled cup with a crenulate or 5-lobed border, with 2 persistent pappus setae, 4-6 mm long, within; deciduous pappus setae about 20, falling separately.

Mexico, Baja California, moist locations, valleys and canyon walls, infrequent, usually flowering February and March.

This plant is easily distinguished from the other species by the broad basal leaves. The cupulate achene resembles that of *M. fendleri*, but in *M. fendleri* there is only one persistent seta. The branching, inflorescence, and slender stems are similar in appearance to *M. clevelandi*.

### 4. MALACOTHRIX CLEVELANDI Gray, Bot. Calif., 1:433. 1876.

Fig. 4

Type.—Near San Diego, Daniel Cleveland (GH, marked, "original Malacothrix Clevelandi n. sp.!" by Gray, 1875. Mounted on same sheet with collections by C. C. Parry and J. G. Lemmon, southern California 1876).

Annual; 1.4 dm tall with a slender tap root; stems 1-several, erect or ascending, usually much branched, loosely paniced, slender (to less than 0.5 mm near apex in some cases), reddish in older portion, appearing glabrous, but occasionally a few thin white hairs present; leaves sessile, thin, essentially glabrous; leaves of basal rosette linear-lanceolate, pinnately lobed to lacinate-pinnatifid, 2.7 cm, occasionally 8 cm long, 5-10 mm wide; cauline leaves more nearly entire, widely scattered, gradually decreasing in size



apically; length of pedunculate part of stem variable, usually 1-3 cm, occasionally 5-7 cm; heads numerous, 3-5 mm broad, 22-70 flowered; involucre narrowly campanulate to cylindrical, upright at maturity, 5-8 mm high; phyllaries green, approximately 1 mm in width, with brownish or purplish tips, inner 9-14 in one rank, 4-6 mm long, outer fewer in number, in one or two ranks, 1-3 mm long; receptacle flattened, without bracts, but with narrow ridges; ligules yellow or occasionally white, only slightly exerted beyond involucre, 3-6 mm in length, 0.5-1 mm broad, tube and limb length approximately equal; style 3-6 mm long, cleft 0.4 mm or less, and covered with fine short hairs .02 mm long; achenes cylindrical, 1.5 mm long, brown, base flattened, surface serrulate, equally 15-16 striate-costate, apex flattened, light in color, surrounded by a pale pectinate rim; pappus white, consisting of an inner deciduous ring of setae plus one or occasionally two persistent outer setae 3.5-4 mm long, and a circle of some 16 elongated white teeth, subequal, 0.05 to 0.15 mm in length.

Back beaches, washes and chaparral slopes up to 6,000 or sometimes 7,000 ft., often occurring on burned-over ground, coastal California from Glenn Co. S. to central Baja California, occasional in Sierra Nevada foothills and mountains of central Arizona. March-June.

Jepson (1925) describes *M. clevelandi* as "few-flowered," while Gray (1876) describes the type as "rather many flowered." On actual count the number of flowers per head was found surprisingly large considering the small inconspicuous appearance of the heads. Sixty-nine was the highest number of flowers found in one head and twenty-two the smallest. The tubes of the corolla tend to separate on drying, while the upper parts of the flowers tend to stick together, probably due to the sticky stigmatic surfaces. The projecting tubes can be readily counted with a dissecting microscope.

5. *MALACOTHRIX FENDLERI* Gray, Smithsonian Contrib. to Knowledge, 5:104. 1853.

Fig. 5

*Lectotype*.—Low sandy banks of the Rio del Norte, New Mexico, Fendler. Designated by Wootton & Standley, Contr. U.S. Nat. Herb., 19:624. 1915. (Presumably at GH, but not seen.) Interpretation here based on the historical specimen of Wright, stony hills round El Paso, 1424 (GH). *M. sonchoides*, Gray, Mem. Amer. Acad. NS 4:113, 1849, non Torr. & Gray.

Annual; 5-30 cm tall, with few to several sparsely leafy erect stems from a basal rosette of leaves; tap root slender, tapering, approximately as long as height of plant; stems green, turning light brown when dry, hollow, terete, glabrous, sparsely branched, main stems 1-40, with 1-5 heads per main branch, 2-10 cm from base to first node, 1-4 cm to second node; basal leaves 2-7.5 cm long, tapering toward base, but with no well-defined petiole, glabrous, or occasionally with flocks of woolly white hairs, sometimes as long as 1 mm, margin pinnately lobed, the lobes bluntly pointed, or with the margin of the main lobes also lobed; cauline leaves decreasing in size apically and becoming more nearly entire; involucre usually 7-10 mm tall (sometimes 5); phyllaries linear-lanceolate, slightly imbricated in about 3 ranks, outer short, subulate, inner lanceolate, often with a red median line, ending in a spot and a few ragged hairs; number of flowers per head 50-80; expanded heads 2-3.5 cm across; receptacle with very slight ridges marking bases of achenes; ligules yellow, occasionally outermost pink-streaked, 10-15 mm long, up to 4 mm broad, achenes 2 mm long, cylindrical, evenly 15-ribbed, dark brown, ribs semi-circular in cross section, surface serrulate, base formed by 5 lighter colored flattened lobes, upper 0.2 mm of achene slightly expanded without ridges, within which is a ring of white shallow teeth, these together with dark outer wall forming a hollow apical cup; pappus setae 24-29, sub-equal, 4-4.5 mm long, deciduous in a ring, with barbellulae as long as 0.14 mm at base, persistent setae usually one, occasionally none.

Deserts, open plains, and washes, northern Mexico, Sonora, western tip of Texas, SE. New Mexico, and southern Arizona. March-May.

6. *MALACOTHRIX SONCHOIDES* (Nutt.) Torr. & Gray, Fl. N. Amer., 2:486, 1843.

Annual, 5-30 cm high from a rosette of pinnatifid leaves; tap root long, tapering, whitish in young plants; secondary roots usually well developed; stems terete, hollow, 1.5-6 mm in diameter at base, green, turning light brown, 1-several from the root crown, glabrous or with few to numerous gland-tipped hairs, branching alternate, cymose; leaves mostly in a basal rosette, 2-8 cm long, usually glabrous, oblanceolate to linear-lanceolate, pinnately cleft to pinnately divided or dentate, individual segments often toothed and spinulose in mature plants; base of leaves linear, tapering with entire margin; cauline leaves sessile, occasionally somewhat auriculate, usually much reduced, occasionally with gland-tipped hairs; principal inflorescence cymose; heads several to numerous, rarely one; flowers fragrant; peduncles 1-7 cm long; receptacle with short scales marking margins of achenes, some with pale hairs; involucre broadly campanulate, 7-12 mm high; outer phyllaries subulate or ovoid in 1-2 ranks, scarcely imbricated, 2-7 mm long, outer margin often with a few glandular hairs; inner phyllaries 0.5-1 cm long, lanceolate, apex acuminate, imbricated in 1-2 series, margins membranaceous, pale, center portion green, apex terminating in a few straggly hairs; heads 1-2.5 cm broad, 40-90 flowered; ligules bright yellow 10-18 mm long, 1-1.5 mm broad, innermost one-third shorter than outer; tube 6-7 mm, with a few short uniseriate hairs present at point where tube joins limb; anthers 3-4 mm; style 9-12 mm, upper half puberulent and somewhat thicker than lower, cleft 0.5-1.5 mm; achenes light brown, 2-4 mm long, cylindric, sometimes slightly curved, base tapering surface slightly roughened, 15 striate, 5 ribs stronger, sometimes wing-like, apex shallow, concave, bordered by a white crenulate border; pappus setae 17-32, all deciduous in a ring.

KEY TO VARIETIES

Pappus setae all deciduous; herbage usually glabrous .....a. var. *sonchoides*  
1-5 pappus setae persistent; herbage usually with glandular hairs .....b. var. *torreyi*

6 a. *M. SONCHOIDES* (Nutt.) Torr & Gray var. *SONCHOIDES*

Fig. 6

*Lectotype*.—Plains of the River Platte in June, Nuttall (GH, mounted on same sheet with Geyer No. 40—automatically the type since it was the only specimen cited). *Leptoseris sonchoides* Nutt., Trans. Amer. Phil. Soc., NS 7:439, 1841.

Achenes 15 striate, with 5 ribs somewhat stronger; pappus setae all deciduous, covered with fine, rather evenly distributed, short barbellulae.

Scattered dry localities, up to 6,000 ft., from Wyoming and central Idaho south through Utah, western Colorado, to northern Arizona and New Mexico, western Nevada, and Mohave Desert in California.

6 b. *M. sonchoides* (Nutt.) Torr. & Gray var. *torreyi* (Gray) comb. nov.

*Lectotype*.—Salt Lake, Utah, 1851, Stansbury ex Torrey (GH—chosen here because species is named for Torrey). *M. torreyi* Gray, Proc. Amer. Acad. Arts Sci., 9:213, 1874.

*M. runcinata* Nelson, Bull. Torr. Bot. Club, 26:485, 1899. *Type*.—Fort Steele, Wyoming, June 18, 1898, Aven Nelson 4819 (R 15450—designated as type by Rocky Mt. Herbarium).\*

Achenes 3-4 mm long, base 5-lobed, surface brown or tan, serrulate, with 5 conspicuously projecting longitudinal striations, with 2 less prominent ridges between each, apex concave, border marked by projection of the 5 stronger ridges, inside these, and alternate with them, 1-5 persistent pappus setae 4.5-6 mm long, and a few white teeth, inside these

\* This has previously been called a synonym of *M. sonchoides* (var. *sonchoides*). However, close examination of the type reveals the presence of glandular hairs, also one persistent pappus seta.

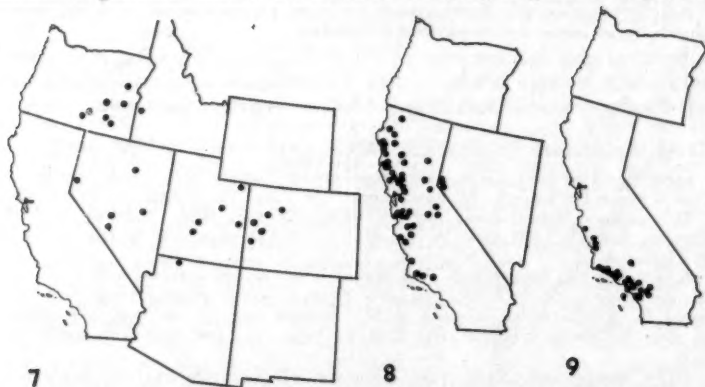


Figs. 4-6.—Geographic distribution of *Malacothrix*. 4. *M. clevelandi*; 5. *M. fendleri*; 6. *M. sonchoides* var. *sonchoides*.

a ring of 17-20 deciduous setae, subequal, 4-7 mm long; barbellulae of persistent setae 0.08-0.09 mm at apex, shorter at base, evenly distributed, and more closely appressed at base; barbellulae of deciduous setae same length at apex and base (up to 0.09 mm), but not regularly spaced, and growing at various angles at base, while more appressed at apex.

Deserts, mesas, and canyons 1,000 to 6,000 ft., scattered localities from SE. Oregon and western Idaho, south through Nevada, Utah, western Colorado to the northern border of Arizona. May - July.

*M. torreyi* is here treated as a var. under *M. sonchoides*. It was found that there was no clear-cut distinction between the two. The presence or absence of glandular hairs is not a reliable character, as glandular hairs seem



Figs. 7-9.—Geographic distribution of *Malacothrix*. 7. *M. sonchoides* var. *torreyi*; 8. *M. floccifera*; 9. *M. saxatilis* var. *tenuifolia*.

to occur occasionally in var. *sonchoides*, and are often very sparse in var. *torreyi*. The shape of the achenes, that is the presence or absence of five wing-like ridges in var. *torreyi* is more pronounced in some plants, and less so in others from another locality, so that this character merges into the five more prominent ridges common in var. *sonchoides*. The presence of persistent pappus setae appears to be the most reliable character to distinguish the two. Thus, plants which have persistent setae are treated as *M. sonchoides* var. *torreyi*, while those with no persistent setae are treated as *M. sonchoides* var. *sonchoides*. With this as the basis of segregation a group of Oregon plants with glandular hairs, previously treated as *M. torreyi*, was identified as *M. sonchoides* var. *sonchoides* because of the lack of persistent pappus setae.

*M. sonchoides* var. *torreyi* resembles *Calycoseris* in the nature of the glandular hairs. However, in *Calycoseris* the achenes are beaked, and the leaves are pinnatifid into linear segments.

7. MALACOTHRIX FLOCCIFERA (DC.) Blake, Contrib. U.S. Nat. Herb.  
22:656. 1924.

Fig. 8

Type.—Douglas, California (Not seen, probably in the Prodomus Herbarium of the De Candolle's in the Delessert Herbarium, Geneva).\* *Senecio flocciferus* DC., Prodr., 6:426. 1837.

*Malacothrix obtusa* Benth., Pl. Hartw., 321. 1849. Type.—Sacramento, California, Hartweg (Kew, not seen\*).

*M. parviflora* Benth., Ibid. Type.—In sylvis prope Santa Cruz, Hartweg (Kew, not seen\*\*).

*M. senecioides* Reiche, Fl. Chile 36, 1910. (Type not seen. Belongs here, fide Babcock, 1947).

Annual, erect, freely branching, 0.5-5 dm high, from a gradually tapering tap root; secondary roots often well developed; stems at first one, later often several from a basal rosette of leaves, slender, considerably branched, terete and hollow, lightly striate, glabrous, green turning light brown or reddish; leaves 1-8 cm long, 4-12 mm broad, oblanceolate to linear-lanceolate, pinnatifid into numerous obtuse dentate segments, circular floccs of white tomentum usually present; stem leaves usually few and reduced, linear, toothed or entire, decreasing in size apically; principal inflorescence cymose; heads numerous, small; peduncles slender, varying in length, subtended by subulate to linear-lanceolate bracts; receptacle with narrow ridges of tissue marking bases of achenes, or these sometimes greatly elongated into thin hairs; involucre 5-8 cm high, green, often streaked or tipped with pink, outer phyllaries subulate, imbricated in 1-3 series; few flowered to 40 or 45 flowered (depending on habitat); outer ligules approximately 10 mm long, white, often with pink or purplish streaks on back, so that heads appear red when closed; inner ligules shorter (approximately 7 mm) white, with throats sometimes yellow, or occasionally ligules all yellow, tube 2.5-3 mm; ligules exserted beyond involucre 5-8 mm; styles barely

\* According to Blake (1924): "De Candolle's description of *Senecio flocciferus*, which was evidently based on imperfect material, agrees well with *Malacothrix obtusa*, and his name is referred to the synonymy of that species by Gray. As this was not a homonym, it is necessary to adopt it in place of *Malacothrix obtusa* Benth."

\*\* Regarding the synonymy of this species Hall (1907) states: "The type specimens of *M. obtusa* and *M. parviflora* have been compared at Kew by Professor W. L. Jepson, who informs me that he is unable to distinguish them by any technical character, although the type of the former has little flock of wool on the leaves, these being absent from the type of *M. parviflora*. He further adds that neither of these types has the persistent setulose teeth crowning the achenes, so characteristic of *M. Clevelandi*."

cleft, upper half puberulent, somewhat exerted beyond inner ligules; uniserate hairs present on base of limb of ligule; anthers approximately 3 mm long, with free ends .75 mm long; achenes plump, usually somewhat curved toward one side, 1.5-1.75 mm long, dark brown, rather shiny, often with 5 ribs more prominent, the others delicate or obscure, surface slightly serrulate, apex concave, with a narrow entire or minutely dentate rim; pappus setae 20-30, all readily deciduous, inclined to fall separately, and with short spine-like barbellulae.

Coast ranges of California from Siskiyou Co. S. to Ventura Co.; Sierra Nevada, Plumas Co., S. to Yosemite; Nevada, vicinity of Lake Tahoe; gravelly hillsides 500 to 7000 ft. April-September. Introduced into Chile.

*M. floccifera* is similar in size of heads and general appearance to *M. clevelandi*, but the differences are numerous: (1) pappus, all deciduous in *M. floccifera*; one or occasionally two hairs persistent in *M. clevelandi*; (2) ligules longer in *M. floccifera* and more exerted beyond phyllaries than in *M. clevelandi*; (3) flocks of wool on leaves usually present in *M. floccifera*; (4) color of ligules usually yellow in *M. clevelandi*, usually white with pink streaks in *M. floccifera*; (5) setulose teeth characteristic of apex of achenes in *M. clevelandi*; absent in *M. floccifera*.

8. *MALACOTHRIX INCANA* (Nutt.) T. & G., Fl. N. Amer., 2:486. 1843.

Decumbent perennial herb, rarely erect, 1-3 dm high from a thick woody tap root, longer than the plant is tall; main stem woody, almost solid, 3-8 mm in diameter, quite leafy, often clothed with a dense white tomentum, secondary branches 1-several, less solid and more slender, often forming dense mats; leaves succulent, 3-10 cm long, up to 18 mm across at the widest point, oblanceolate, occasionally entire or undulate, usually pinnatifid into a few obtuse lobes; lower leaves persistent after they become dry; heads few to several, solitary, turbinate, 1.5-2.5 cm broad, by approximately the same length, 50-100 flowered; scapes 2-15 cm long, hollow, usually leafless, but often with a few bracts along length, gradually expanded at apex and bearing numerous sparsely imbricated subulate phyllaries, 3-5 mm long; inner phyllaries linear-lanceolate, 10-12 mm long, green, often tinged with pink, apex obtuse; receptacle glabrous, 0.5-1 cm broad when dry; ligules yellow, 6-10 mm, apex shallowly 5-dentate, tube 3-6 mm, with numerous uniserate hairs present at region where it joins limb; style 8-9 mm, barely if at all cleft, upper half puberulent; anthers 3-3.5 mm long; achenes 1.5-1.75 mm long, dark brown, cylindrical, base tapering, sides lightly 12-15 striate, apex truncate, with an inconspicuous rim; pappus setae about 35, all deciduous, 6 mm long.

KEY TO VARIETIES

Leaves clothed with matted white wool, lobed or pinnatifid .....a. var. *incana*  
Leaves glabrous when mature, margins entire or occasionally undulate .....b. var. *succulenta*

8 a. *M. INCANA* (Nutt.) T. & G. var. *INCANA*.

*Type*.—San Diego, California, Nuttall (GH, mounted on same sheet with collections by Greene from Santa Cruz and San Miguel. Automatically the type as it was the only specimen cited.) *Malacomeris incanus* Nutt., Trans. Amer. Philos. Soc., Ser. 2, 7:435, 1841.

California, San Miguel, Santa Rosa, Santa Cruz, and San Clemente Islands, and sand dunes along the coast of San Luis Obispo and Santa Barbara counties. April-September.

8. b. *M. incana* (Nutt.) T. & G. var. *succulenta* (Elmer) comb. nov.

*Type*.—Santa Barbara, May 1902, A. D. E. Elmer 3639 (S 60894—as designated by Elmer).



Sand dunes, Santa Barbara Co., California, between Guadalupe and Surf. May-July.

9. *MALACOTHRIX FOLIOSA* Gray, Syn. Fl. N. Am., 1, Part II, Supplement, p. 455, 1886.

Annual, 5-40 cm high from a somewhat thickened tap root; stems glabrous, sparsely to freely branching, and quite leafy; leaves oblong-lanceolate, 0.5-6 cm, glabrous, sessile, and somewhat clasping, pinnately toothed to pinnately parted, with apex and segments acute, sometimes quite reduced; inflorescence cymose-paniculate, heads numerous, 0.5-2 cm across; involucre campanulate, phyllaries in 2-4 ranks, outer ones often broad, 0.5 cm or less in width, inner, 0.5-1 cm long, linear-lanceolate; heads 30-90 flowered; ligules yellow, 6-8 mm long; receptacle naked or with short bracts; achenes 2 mm; cylindric, 15 ribbed, with 5 ribs more prominent, apex with numerous deciduous pappus setae, 5-6 mm long.

KEY TO VARIETIES

- Leaves succulent, lobes rather obtuse; inner phyllaries 4-5 mm long .....a. var. *indecora*  
 Leaves not succulent, lobes acute; inner phyllaries 5-10 mm long .....  
 Lobes and apex of leaves short, thick .....b. var. *squalida*  
 Lobes and apex of leaves attenuated .....c. var. *foliosa*

9 a. *M. foliosa* Gray var. *indecora* (Greene) comb. nov.

Type.—Santa Cruz I., California, July and August 1886, Edward L. Greene (CAS 49859—labeled by Greene as the type, although Hall believes CAS 49858 was the plant upon which Greene based his description). *M. indecora* Greene, Bull. Cal. Acad. Sci. 2:152, 1886.

Forming dense mats 5-10 cm deep; however, sometimes erect, slender, and even 4 dm. tall; leaves succulent, pinnately lobed, the lobes mostly obtuse; involucre 6 or 7 mm high.

Rocky islets and promontories, Santa Cruz, San Miguel, and San Nicholas Islands. April-September.

Specimens examined.—California. SANTA BARBARA Co.: San Miguel I., Greene (CAS); Santa Cruz I., Greene (CAS, DS); M. W. Williams 87 (POM). VENTURA Co.: San Nicholas I., Trask (LAM, UC).

9 b. *M. foliosa* Gray var. *squalida* (Greene) comb. nov.

Type.—Rocky promontory above Prisoner's Harbor, Santa Cruz I., July and August 1886, E. L. Greene (CAS 49863, marked "type" and UC 92210 marked "part of type"; DS 117608, isotype). *M. squalida* Greene, Bull. Cal. Acad. Sci., 2:152, 1886.

Compact growth, up to about 2 dm in height; stems stout, leaves clasping, with short acute lobes.

San Miguel, Santa Cruz, and Santa Barbara Islands, California. April-August.

Specimens examined.—California. LOS ANGELES Co.: Santa Barbara I., Moran 824 (CAS, DS); Trask (UC).

9 c. *M. FOLIOSA* Gray var. *FOLIOSA*.

Type.—San Clemente Island, April 1885, Nevin and Lyon (GH—automatically the type as this was the only collection cited at time of publication. DS 117575, CAS 49857 and UC 92211, isotypes).

*M. insularis* Greene, Bull. Cal. Acad. Sci. 4:194, 1885. Type.—Mexico, Coronados I., May 16, 1885, E. L. Greene (CAS 49862 marked "type," and CA 49953, DS 848 and UC 92215 marked "part of type").

Plants up to 4 dm tall; stems slender, leafy; leaves with attenuate acute lobes, not succulent.

San Clemente, Santa Barbara and Santa Cruz Islands. March-August.

*Specimens examined*.—California. LOS ANGELES CO.: San Clemente I., Peirson 3463 (DS, UC), Munz 6612 (POM, UC), Murbarger 164 (UC), Abrams & Wiggins 339 (CAS, DS, UC), House & Grumbles (SC); Santa Barbara I., Bond (UC), Elmore 370 (AHFH), Abrams & Wiggins 304 (DS, UC). SANTA BARBARA CO.: Santa Cruz I., Brandegee (UC). Mexico. BAJA CALIFORNIA: Coronados Islands, Anthony (UC), Pierce (POM).

10. *MALACOTHRIX BLAIRII* (Munz & Jtn.) Munz, Man. So. Calif. Bot., 591, 601, 1935.

Type.—Rocky wall of canyon, San Clemente Island, California, autumn 1923, E. G. Blair (POM 20492, as designated by Munz & Johnston). *Stephanomeria Blairi* Munz & Johnston, Bull. Torr. Bot. Club 51:301. 1924.

Perennial, broad-leaved shrub, about 1-1.5 m tall, by approximately 1 m wide; stems woody, straggly, 8-10 mm thick, very brittle, becoming light brown, and marked by persistent hardened bases of petioles; young flowering stems often with fine closely appressed white hairs; leaves crowded closely together, up to 13 cm long by 7 cm broad, reduced up the stem, glabrate, light green, firm, but rather thin, and with conspicuous venation, ovate, tapering toward base, into a short petiole, margins irregularly sinuate or lobulate, apex rounded; inflorescence terminal, stiff, paniculate, compact, 5-20 cm long, 8-10 cm thick, branches strict or ascending, several to many headed; peduncles 2-4 mm long, covered with numerous short glandular hairs, subtended by subulate bracts approximately 2 mm long; heads 8-14 mm high; involucre cylindrical, inner phyllaries 6-10 mm long, about equal, 1-2 mm broad, sparingly imbricated, pale green, tinged with rose, outer phyllaries green, subulate to lanceolate, 1-3 seriate, extending somewhat down the peduncle; receptacle glabrous, heads 6-15 flowered; ligules rose-colored, 10-12 mm long (tube 3.5 mm and limb 6.5 mm), puberulent outside, tip 5-dentate, anthers about 5 mm long, style puberulent, cleft 1 mm, often exerted beyond ligule 1-2 mm; achenes 3-3.5 mm long, 0.5-0.75 mm broad, light brown, pentangular, faces with 1-3 shallow longitudinal grooves, surfaces almost smooth, apex truncate, marked by a double rim, pappus setae 30-40, readily deciduous, sub-equal, 4-6 mm long, with antrorsely directed barbellulae.

San Clemente Island, California, endemic, both sides of the island on the steep rocky canyon walls.

*Specimens examined*.—California. LOS ANGELES CO.: San Clemente Island, House & Grumbles (SC, POM), Munz 6681 (POM), Murbarger 195 (UC). CULTIVATED SPECIMEN: Univ. of Calif. Hort. Genetics No. 466, seeds collected by Nell Murbarger.

The tips of the ligules were originally described as 2-3-dentate. They give this impression due to the fact that the ligule acts as a sheath inclosing the anthers and style, and when it splits at maturity the lobes have a tendency to stick together. However, when the apex of a ligule is flattened out it is evident that actually it is five-dentate.

This shrub, with its broad leaves and pink inflorescences, makes an attractive appearance. The author was informed by Dr. Herbert L. Mason, of the University of California, that he has grown *M. blairii* successfully for a number of years in his garden in Berkeley.

11. *MALACOTHRIX SAXATILIS* (Nutt.) T. & G., Fl. N. Am., 2:486, 1843.

Perennial, suffrutescent, with 1-several erect or decumbent stems, 3-20 dm tall, arising from crown of an elongated, often thickened, tap root; stems freely branching, glabrous, or covered with white tomentum, hollow, woody in older portions, and up to 2 cm in diameter, often reddish- or purplish-brown toward base, leafy to rather naked; leaves variable as to marginal indentation, cauline, sessile, covered with white tomentum, or tomentulose when young, becoming glabrous, succulent or not succulent, alternate, or sometimes fascicled, lower leaves 2-12 cm long, lanceolate or spatulate, entire, coarsely toothed or pinnatifid, or irregularly bipinnatifid into numerous narrow linear divisions; upper leaves linear-lanceolate to spatulate, often entire, decreasing in size apically; inflorescence loosely cymose-paniculate; peduncles of varying length (0.5-10 cm), with subulate bracteoles often present, especially near apex; heads few to quite numerous; 1-4 cm broad; phyllaris in 3 or 4 series, woolly or glabrous, outer subulate, inner 2-10 mm in length, lanceolate, attenuated, with purplish midrib; receptacle flat, surface glabrous, pitted; number of flowers per head 51-95; outer ligules 1-1.5 cm long, approximately 4 mm broad, tube 6 mm long, often streaked with pink or purple on abaxial side; inner ligules slightly shorter, white, occasionally yellow; anther tube marked with 5 purplish-red longitudinal lines; style 1-1.5 cm, exceeding stamens, 1-2 mm, white; achenes brown, columnar, short-tapering at base, 2 mm or less in length, surface serrulate, 12-15 longitudinal ridges present, with 5 ribs somewhat more prominent; apex flattened, white, bordered by a double row of fine white teeth; pappus setae 26-30, subequal, 4-6 mm long, all deciduous in a ring; lower barbellulae somewhat longer and more spreading than upper.

## KEY TO VARIETIES

- Leaves bi-pinnatifid into numerous linear segments .....a. var. *implicata*  
 Leaves entire, or pinnatifid with broad segments.  
 Herbage hoary throughout with a thick white tomentum .....b. var. *arachnoidea*  
 Herbage essentially glabrous.  
 Lower leaves entire or only slightly toothed, oblanceolate .....c. var. *saxatilis*  
 Lower leaves toothed with acute apex and segments .....d. var. *tenuifolia*

11 a. *M. SAXATILIS* (Nutt.) T. & G. var. *IMPLICATA* (Eastw.) Hall,  
Univ. Calif. Pub. Bot. 3:269, 1907. "Queen Daisy"

*Type*.—Sand and wind carved cliffs, San Nicolas Island, California, April 1897, Blanche Trask (CAS 49861—description based on this collection as stated by Miss Eastwood). *M. implicata* Eastwood, Proc. Calif. Acad. Sci., Ser. III, 1:113, 1898.

Bluffs and canyon walls, Anacapa, San Miguel, San Nicolas, Santa Barbara, Santa Cruz, and Santa Rosa Islands, California. April-September.

11. b. *M. saxatilis* (Nutt.) T. & G. var. *arachnoidea* (McGregor)  
comb. nov.

*Type*.—Carmel Valley, Monterey Co., California, July 1, 1906, Ernest A. McGregor 1575 (S 60891—designated by McGregor). *M. arachnoidea* McGregor, Bull. Torr. Bot. Club, 36:605, 1909.

Herbage hoary throughout with a dense white tomentum; leaves lanceolate, sessile, lower ones 4-10 cm long, sometimes slightly dentate, upper leaves entire, decreasing in size apically; heads numerous, when expanded 2-3.5 cm across; involucre 1.5-2 cm high, hemispherical in bud, campanulate in flower; outermost phyllaries subulate, woolly, often extending down stem for about 0.5 cm, and not imbricated, innermost linear-lanceolate, more nearly glabrous, sparingly to well imbricated; heads 55-95 flowered.

Carmel Valley, Monterey Co., California. March-October.

11 c. *M. SAXATILIS* (Nutt.) T. & G. var *SAXATILIS*.

*Type*.—Santa Barbara, California, on shelving rocks near the sea, Nuttall (GH, specimen marked “\**Leucoseris* \**saxatilis*,” and *M. saxatilis* Torr. and Gray”). *Leucoseris saxatilis* Nutt., Trans. Amer. Philos. Soc., Ser. 2, 7:440, 1841.

*Malacothrix commutata* Torr. & Gray, Fl. N. Amer., 2:487 1843. *Type*.—California, Douglas (GH)—Authentic specimen labeled by Gray as *M. saxatilis*. On the same sheet the names of *M. commutata*, *Leucoseris Californica*, *Hieracium*? *Californica* and *Sonchus Californica* appear.)

Plants herbaceous, stems decumbent, 3-6 cm tall, leafy throughout; leaves somewhat succulent, lower leaves oblanceolate entire, or lanceolate and slightly toothed, upper leaves lanceolate, entire; flowering heads about a dozen, rather large.

Occurs along the coastal bluffs of Santa Barbara and San Luis Obispo counties, California. April-September.

11 d. *M. SAXATILIS* (Nutt.) T. & G., var. *TENUIFOLIA* (Nutt.) Gray, Syn. Fl. N. Amer., 1, pt. 2, p. 423. 1884.

## Fig. 10

*Type*.—*Leucoseris tenuifolia* Nutt. was based on an immature plant seen growing at Santa Barbara, California, by Nuttall. Whereabouts of his specimen not ascertained. Interpretation here based on Coulter's collection from California (GH) which Gray (1884) cited as being the earliest collection, but which is obviously not the historical type on which the concept was based. *Leucoseris tenuifolia* Nutt., Trans. Amer. Phil. Soc. NS 7:440, 1841. *Malacothrix tenuifolia* (Nutt.) T. & G. Fl. N. Am., 2:487, 1843.

*M. altissima* Greene, Bull. Calif. Acad. Sci. 1:195, 1885. *Type*.—Tehachapi, Kern Co., California, July 1884, M. K. Curran (CAS 49856—only collection cited).

*M. saxatilis* (Nutt.) T. & G., var. *tenuissima* Munz, Man. So. Calif. Bot. p. 601, 1935. *Type*.—Glen Ivy trail to Santiago Peak, Santa Ana Mts., Orange Co., California, June 14, 1923, P. A. Munz 7101 (POM 17952).

Up to 17 dm tall; inflorescence freely cymose-paniculate, numerous flowered, with flowers decreasing in size as they increase in number, due to continued branching; leaves glabrous, not succulent, lowermost up to 12 cm long, by about 5 cm broad, considerably varied in width and degree of segmentation, pinnately parted with coarse acute segments, these often somewhat attenuated; upper leaves narrow, often entire, linear-lanceolate, usually occurring in fascicles after the first season.

Coast ranges of California from southern Monterey County south to Orange County and Santa Catalina Island. Early spring to late fall.

The leaf character of this species is quite variable. Var *saxatilis* has been treated in a restricted sense. Only those specimens are cited which conform to the original description of Torrey and Gray (1843), that is, “leaves fleshy, linear-oblong, obtuse, mostly entire.”

*M. saxatilis* var. *tenuifolia* is the most widely occurring variety, and also the most variable. In Monterey County and San Luis Obispo County, California, it seems to intergrade somewhat with var. *arachnoidea*, in that the leaves are more nearly entire, and covered with a thin white tomentum. Plants having quite a different aspect are represented in two collections by John Thomas Howell from “Rocky coastal bluff, 1 mi. s.e. of Gaviota Pass.” No. 5182 (POM 179715) shows broad leaves with numerous broad segments, while 5181 (CAS 180995), growing only a few feet away, has narrow leaves with linear segments. The narrow-leaved plant appears to be close to var. *implicata*; however, both plants are here treated as var. *tenuifolia*.

*M. altissima* is listed as a synonym of var. *tenuifolia*. In Greene's (1886) original description of the species he states that *altissima* is: "The largest species of the genus, and of the same group as the two following [*M. saxatilis* and *M. tenuifolia*] which are suffrutescent . . ." In keys *saxatilis* and *altissima* have been separated on the basis of *altissima* being listed as an annual or biennial, and *saxatilis* a perennial. This is obviously unsatisfactory, and as far as I can discover the two are indistinguishable on this basis. The foliage and general aspect of the plant the first year is distinct in that the leaves are large, single at the nodes, and the inflorescence is less branched, with the heads large. In succeeding years the new foliage is fasciated at the site of the old leaves, while the branching becomes more ramified and the heads smaller and more numerous. *M. altissima* is described by Greene as the largest species of the genus, "3 to 6 ft. high." Hall (1907) describes var. *tenuifolia* as 1 to 2.5 m high, and *altissima* as 1 to 2 m high. The type of *M. altissima* seems to bear out the above observations, in that it is indistinguishable from *M. saxatilis* var. *tenuifolia*.

## REFERENCES

- BABCOCK, ERNEST BROWN 1947—The Genus *Crepis*. Univ. Calif. Publ. Bot. 21, 22.
- BAILEY, L. H. 1941—Hortus Second.
- BENTHAM, GEORGIUS 1839—*Plantae Hartwegianae imprimis Mexicanas*, p. 321.
- BLAKE, S. F. 1924—New American Asteraceae. Contr. U.S. Nat. Herb. 22:656.
- BRANDEGEE, KATHERINE 1893—The botanical writings of Edward L. Greene. Zoe 4:63-103.
- 1894—The dates of Botany Beechey, Flora Boreali-Americana, and Torrey & Gray's Flora. *Ibid.* 4:369-372.
- DE CANDOLLE, AUG. PYRAMO 1837—*Prodromus Systematis Naturalis Regni Vegetabilis* 6:426.
- 1838—*Ibid.*, 7:192, 234-235.
- EASTWOOD, ALICE 1898—Studies in the Herbarium and the Field. Proc. Calif. Acad. Sci., Ser. III, 1:113.
- EATON, DANIEL C. 1841—Compositae, in Clarence King's Report of the Geological Exploration of the Fortieth Parallel (Vol. V, Botany. By Sereno Watson, aided by Prof. Daniel C. Eaton, and others.) p. 201.
- ELMER, A. D. E. 1905—New and Noteworthy Western Plants. Bot. Gaz. 39:44.
- GRAY, ASA 1853—*Plantae Wrightianae Neo-Mexicanae*. Part II. An Account of a Collection of Plants made by Charles Wright, A.M., in Western Texas, New Mexico, and Sonora, in the years 1851 and 1852. Smithsonian Contributions to Knowledge 5:104-105.
- 1849—*Plantae Fendlerianae Novi-Mexicanae*. Mem. Amer. Acad. N.S. 4:113.
- 1860—*Malacothrix crepoides*, in J. G. Cooper's Catalogue of plants collected in Washington Territory. Pacific R.R. Rept., 12:53.
- 1874—Notes on Compositae and Characters of Certain Genera and Species. Proc. Amer. Acad. 9:187-218.
- 1876—Botany of California. Geol. Surv. Calif. 1:433.
- 1884 AND SUPPLEMENT 1886—Synoptical Flora of North America. 1:422, 423; and 1, Part 2, Supplement p. 455.
- GREENE, EDWARD LEE 1886—Studies in the botany of California and parts adjacent. Bull. Cal. Acad. Sci. 1:194-95 and 2:152.
- HALL, HARVEY MONROE 1907—Compositae of Southern California. Univ. Calif. Pub. Bot. 3:263-269.



- HELLER, A. A. 1906—Botanical Exploration in California. *Muhlenbergia* 2:147.
- JACKSON, B. DAYDON 1893-1953—Index Kewensis and Supplements.
- JEPSON, WILLIS LINN 1925—A manual of the flowering plants of California.
- KEARNEY, THOMAS ET AL. 1951—Arizona Flora.
- LANJOUW, J. AND F. A. STAFLEU 1954—Index Herbariorum.
- LYON, WILLIAM S. 1886—The flora of our southwestern Archipelago. *Coulter's Bot. Gaz.* 11:353.
- MCGREGOR, ERNEST A. 1909—Two new spermatophytes from California. *Bull. Torrey Bot. Club* 36:605.
- MUNZ, PHILIP A. 1935—A manual of Southern California botany.
- AND IVAN M. JOHNSTON 1924—Miscellaneous Notes on Plants of Southern California—III. *Ibid.* 51:301.
- NELSON, AVEN 1899—New Plants from Wyoming—X. *Bull. Torrey Bot. Club* 26:485.
- NUTTALL, THOMAS 1841—Descriptions of new species and genera of plants in the natural order of the Compositae, collected in a tour across the continent to the Pacific. *Trans. Amer. Philos. Soc.* NS 7:435, 438-441.
- PECK, MORTON E. 1941—A manual of the higher plants of Oregon.
- RYDBERG, P. A. 1922—Flora of the Rocky Mountains and adjacent plains.
- STERN, WILLIAM T. 1939—Dates of Publication of de Candolle's *Prodrromus*. *Candollea* 7:1-4.
- TJEDSTRÖM, IVAR, AND SISTER TERESITA KITTELL 1941—A Flora of Arizona and New Mexico.
- TORREY, JOHN 1852—Catalogue of Plants Collected by the Expedition, in Howard Stansbury's Exploration and Survey of the Valley of the Great Salt Lake of Utah, Appendix D, Botany.
- 1859—Botany of the Boundary, in William H. Emory's Report on the United States and Mexican Boundary Survey, 2:106.
- AND ASA GRAY 1843—A flora of North America, 2:486, 487.
- WOOTON, E. O., AND PAUL C. STANDLEY 1915—Flora of New Mexico. *Contr. U.S. Nat. Herb.* 19:624.

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